THE HOPE REPORTS

VOL. I

1893—1897

EDITED BY

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EDWARD B. POULTON, M.A., F.R.S.

HOPE PROFESSOR OF ZOOLOGY IN THE UNIVERSITY OF OXFORD

Oxford

PRINTED FOR PRIVATE CIRCULATION

BY HORACE HART, PRINTER TO THE UNIVERSITY

1897

5 Insects

The Smithsonian Institution

Washington

With the compliments of E. B. Poulton

Aug 24 / 1897.

THE MAKERS OF THE HOPE DEPARTMENT
OXFORD UNIVERSITY MUSEUM

With Professor Poulton's Compliments

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PREFACE

THE Hope Department is not likely to contribute largely to the preparation for examinations which is at present the most conspicuous function of the University and Colleges of Oxford. It is hoped that public lectures, delivered from time to time, may act as some incentive towards the study of natural history, and that, out of the numerous subjects of the Final Honour School in Animal Morphology, those few which can be appropriately illustrated from the Hope Collections, may be usefully expounded in short courses.

The chief duty of the Department must always be the care and the proper arrangement and display of the vast collection of insects of all orders which we owe in the first place to the munificence of the Rev. Frederick William Hope. From the discharge of this duty, if it is to be discharged adequately, results must follow which, it is claimed, give to the Department a meaning and significance in the life of our ancient University. In the present state of Zoological Science, it is impossible to make use of existing knowledge in the careful study of a large amount of material without adding to that knowledge. Research after the various kinds of knowledge which have been prized by mankind during successive ages was of old the prominent function of the University; and although obscured during the recent generations by

excessive devotion to the examination system, may still be claimed as an academic duty and high privilege second to no other in importance. And signs are not wanting that the University of Oxford is in this respect tending towards the ancient ideals, and, while unwilling to yield any of the obvious advantages of modern educational systems, is also inclined to encourage learning and original research.

I therefore determined to follow the example of my friend and colleague the Linacre Professor, and issue from time to time volumes of Reports from the Department, containing reprints of the various memoirs which have been written in connexion with it. The present volume, the first of the series of Hope Reports which I trust will follow, is the outcome of four years' work. During these years much time and attention has been occupied in obtaining increased space and warmth, as well as many other improvements which the growth of the collections had rendered necessary. It is therefore to be expected that the succeeding volumes will appear at shorter intervals, now that these improvements have been effected.

The lines of research which can be favourably pursued in the Hope Department are, in addition to the investigation of insect form, function, and classification, those general sides of Zoological Science for which insects afford some of the best illustrations—such wide subjects for instance as evolution, natural selection, variation, and the numerous problems included in the phrase relation to environment.

The memoirs dealing with these latter subjects, being of more general interest, are placed first in the following arrangement, and, while the works of each author are kept together, those which deal with general subjects are in each case placed first. Two memoirs, No. 6 and

No. 12, describe work which was done before June, 1893, but publication itself took place after that date. In all other cases, as well as in a large part of No. 12, the researches were conducted between June, 1893, and the present date.

The Reports of the Department for the years 1895 and 1896 are included as Nos. 18 and 19. It is intended to include the Reports of all future years in the forthcoming volumes, so that a continuous account of the progress of the Department will be registered.

This volume, and still more the volumes which will follow, are the evidence that the Hope Department is a centre of activity, and counts as one of the forces which are doing important academic work in Oxford, even though its part in teaching for examinations must be a small one.

The Plate at the beginning of this volume represents the makers of the Hope Department—the Rev. Frederick William Hope, F.R.S., who presented his vast collections and complete entomological library to the University, founded the Chair, and continued until his death to purchase fresh materials to add to those which he had already given; Ellen Hope, his wife, who carried on the work, purchasing and presenting many collections of the utmost value, endowed the Keepership of Engraved Portraits, the Collections, and Library, and added to the endowment of the Chair; and John Obadiah Westwood, the first Hope Professor, whose great name and fame enriched the Hope Collections from all parts of the world, who added largely to them from his own private collections, and described an immense number of species, the types of which are among the most valued treasures of the Department.

I have to thank Mr. Alfred Robinson, of the Museum,

for his skilful and careful work in preparing the design which surrounds the three portraits. The insects represented were described and figured by Professor Westwood in the 'Thesaurus Entomologicus,' and their types are in the Hope Department. The uppermost insect is Euchrysia cleptidea, from Adelaide (Plate XXVI, Fig. 3 of the 'Thesaurus'): that on the left side is Solenura telescopica, from Java (Plate XXVI, Fig. 10). Both these insects are much enlarged, the originals being minute parasitic Hymenoptera belonging to the Chalcididae. The butterfly on the right side is Hesperia (Oxynetra) Zambesiaca, from the Zambesi (Plate XXXIV, Fig. 9). It is of the natural size. The left-hand beetle is Chlamydopsis duboulai, from Australia (Plate III, Fig. 7), the right hand Zygaenodes diopsideus, captured by Dr. A. R. Wallace at Sarawak, Borneo (Plate V, Fig. 5). Both are represented many times the natural size.

The portraits were reproduced from engravings of Mr. and Mrs. Hope and a photograph of Professor Westwood, all kindly lent for the purpose by Miss Swann.

EDWARD B. POULTON.

Hope Department of Zoology,
University Museum, Oxford,
June 14, 1897.

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British Association for the Advancement of Science.

LIVERPOOL, 1896.

ADDRESS

TO THE

ZOOLOGICAL SECTION

BY

PROFESSOR E. B. POULTON, M.A., F.R.S., F.L.S.,

PRESIDENT OF THE SECTION.

A NATURALIST'S CONTRIBUTION TO THE DISCUSSION UPON THE AGE OF THE EARTH.

A VERY brief study of the proceedings of this Section in bygone years will show that Presidents have exercised a very wide choice in the selection of subjects. At the last Meeting of the Association in this city in 1870 the Biological Section had as its President the late Professor Rolleston, a man whose remarkable personality made a deep impression upon all who came under his influence, as I have the strongest reason for remembering, inasmuch as he was my first teacher in zoology, and I attended his lectures when but little over seventeen. His address was most characteristic, glancing over a great variety of subjects, literary as well as scientific, and abounding in quotations from several languages, living and dead. A very different style of address was that delivered by the distinguished zoologist who presided over the Meeting. Professor Huxley took as his subject 'The History of the Rise and Progress of a Single Biological Doctrine.'

Of these two types I selected the latter as my example, and especially desired to attempt the discussion, however inadequate, of some difficulty which confronts the zoologist at the very outset, when he begins to reason from the facts around him—a difficulty which is equally obvious and of equal moment to the highly trained investigator and the man who is keenly interested in the results obtained by others, but cannot himself lay claim to the position and authority of a skilled observer—to the naturalist and to one who follows some other branch of knowledge, but is interested in the progress of a sister science.

Two such difficulties were alluded to by Lord Salisbury in his interesting presidential address to the British Association at Oxford in 1894, when he spoke of 'two of the strongest objections to the Darwinian explanation' of evolution—viz. the theory of natural selection—as appearing 'still to retain all their force.' The first of these objections was the insufficiency of the time during which the earth has been in a habitable state, as calculated by Lord Kelvin and Professor Tait, 100 million years being conceded by the former, but only 10 million by the latter. Lord Salisbury quite rightly stated that for the evolution of the organic world as we know it by the slow process of natural selection at least many hundred million years are required; whereas, 'if the mathematicians are right, the biologists cannot have what they demand. . . . The jelly-fish would have been dissipated in steam long before he had had a chance of displaying the advantageous variation which was to make him the ancestor of the human race.'

The second objection was that 'we cannot demonstrate the process of natural selection in detail; we cannot even, with more or less ease, imagine it.' 'In natural selection who is to supply the breeder's place?' 'There would be nothing

but mere chance to secure that the advantageously varied bridegroom at one end of the wood should meet the bride, who by a happy contingency had been advantageously varied in the same direction at the same time at the other end of the wood. It would be a mere chance if they ever knew of each other's existence—a still more unlikely chance that they should resist on both sides all temptations to a less advantageous alliance. But unless they did so the new breed would never even begin, let alone the question of its perpetuation after it had begun.'

Professor Huxley, in seconding the vote of thanks to the President, said that he could imagine that certain parts of the address might raise a very good discussion in one of the Sections, and I have little doubt that he referred to these criticisms and to this Section. When I had to face the duty of preparing this address, I could find no subjects better than those provided by Lord Salisbury.

At first the second objection seemed to offer the more attractive subject. It was clear that the theory of natural selection as held by Darwin was misconceived by the speaker, and that the criticism was ill-aimed. Darwin and Wallace, from the very first, considered that the minute differences which separate individuals were of far more importance than the large single variations which occasionally arise—Lord Salisbury's advantageously varied bride and bridegroom at opposite ends of the wood. In fact, after Fleeming Jenkins's criticisms in the 'North British Review' for June 1867, Darwin abandoned these large single variations altogether. Thus he wrote in a letter to Wallace (February 2, 1869): 'I always thought individual differences more important; but I was blind, and thought single variations might be preserved much oftener than I now see is possible or probable. I mentioned this in my former note merely because I believed that you had come to a similar conclusion, and I like much to be in accord with you.'[1] Hence we may infer that the other great discoverer of natural selection had come to the same conclusion at an even earlier date. But this fact removes the whole point from the criticism I have just quoted. According to the Darwin-Wallace theory of natural selection, individuals sufficiently advantageously varied to become the material for a fresh advance when an advance became necessary, and at other times sufficient to maintain the ground previously gained—such individuals existed not only at the opposite ends of the wood, but were common enough in every colony within its confines. The mere fact that an individual had been able to reach the condition of a possible bride or bridegroom would count for much. Few will dispute that such individuals 'have already successfully run the gauntlet of by far the greatest dangers which beset the higher animals [and, it may be added, the lower animals also]—the dangers of youth. Natural selection has already pronounced a satisfactory verdict upon the vast majority of animals which have reached maturity.'[2]

But the criticism retains much force when applied to another theory of evolution by the selection of large and conspicuous variations, a theory which certain writers have all along sought to add to or substitute for that of Darwin. Thus Huxley from the very first considered that Darwin had burdened himself unnecessarily in rejecting *per saltum* evolution so unreservedly.[3] And recently this view has been revived by Bateson's work on variation and by the writings of Francis Galton. I had at first intended to attempt a discussion of this view, together with Lord Salisbury's and other objections which may be urged against it; but the more the two were considered, the more pressing became the claims of the criticism alluded to at first—the argument that the history of our planet does not allow sufficient time for a process which all its advocates admit to be extremely slow in its operation. I select this subject because of its transcendent importance in relation to organic evolution, and because I hope to show that the naturalist has something of weight to contribute to the controversy which has been waged intermittently ever since Lord Kelvin's paper 'On Geological Time'[4] appeared in 1868. It has been urged by the great worker and teacher who occupied the Presidential Chair

[1] *Life and Letters*, vol. iii.
[2] Poulton, *Colours of Animals*, p. 308.
[3] See his letter to Darwin, November 23, 1859: *Life and Letters*, vol. ii.
[4] *Trans. Geol. Soc.*, Glasgow, vol. iii. See also 'On the Age of the Sun's Heat,' Macmillan, March 1862: reprinted as Appendix to Thomson and Tait, *Natural Philo-*

of this Association when it last met in this city that biologists have no right to take part in this discussion. In his Anniversary Address to the Geological Society in 1869 Huxley said: 'Biology takes her time from geology. . . . If the geological clock is wrong, all the naturalist will have to do is to modify his notions of the rapidity of change accordingly.' This contention is obviously true as regards the time which has elapsed since the earliest fossiliferous rocks were laid down. For the duration of the three great periods we must look to the geologist; but the question as to whether the whole of organic evolution is comprised within these limits, or, if not, what proportion of it is so contained, is a question for the naturalist. The naturalist alone can tell the geologist whether his estimate is sufficient, or whether it must be multiplied by a small or by some unknown but certainly high figure, in order to account for the evolution of the earliest forms of life known in the rocks. This, I submit, is a most important contribution to the discussion.

Before proceeding further it is right to point out that obviously these arguments will have no weight with those who do not believe that evolution is a reality. But although the causes of evolution are greatly debated, it may be assumed that there is no perceptible difference of opinion as to evolution itself, and this common ground will bear the weight of all the zoological arguments we shall consider to-day.

It will be of interest to consider first how the matter presented itself to naturalists before the beginning of this controversy on the age of the habitable earth. I will content myself with quotations from three great writers on biological problems—men of extremely different types of mind, who yet agreed in their conclusions on this subject.

In the original edition of the 'Origin of Species' (1859), Darwin, arguing from the presence of trilobites, Nautilus, Lingula, &c., in the earliest fossiliferous rocks, comes to the following conclusion (pages 306, 307): 'Consequently, if my theory be true, it is indisputable that before the lowest Silurian stratum was deposited long periods elapsed, as long as, or probably far longer than, the whole interval from the Silurian age to the present day; and that during these vast yet quite unknown periods of time the world swarmed with living creatures.'

The depth of his conviction in the validity of this conclusion is seen in the fact that the passage remains substantially the same in later editions, in which, however, Cambrian is substituted for Silurian, while the words 'yet quite unknown' are omitted, as a concession, no doubt, to Lord Kelvin's calculations, which he then proceeds to discuss, admitting as possible a more rapid change in organic life, induced by more violent physical changes.[1]

We know, however, that such concessions troubled him much, and that he was really giving up what his judgment still approved. Thus he wrote to Wallace on April 14, 1869: 'Thomson's views of the recent age of the world have been for some time one of my sorest troubles. . . .' And again, on July 12, 1871, alluding to Mivart's criticisms, he says: 'I can say nothing more about missing links than what I have said. I should rely much on pre-Silurian times; but then comes Sir W. Thomson, like an odious spectre.'

Huxley's demands for time in order to account for pre-Cambrian evolution, as he conceived it, were far more extensive. Although in 1869 he bade the naturalist stand aside and take no part in the controversy, he had nevertheless spoken as a naturalist in 1862, when, at the close of another Anniversary Address to the same Society, he argued from the prevalence of persistent types 'that any admissible hypothesis of progressive modification must be compatible with persistence without progression through indefinite periods;' and then maintained that 'should such an hypothesis eventually be proved to be true . . . the conclusion will inevitably present itself that the Palæozoic, Mesozoic, and Cainozoic faunæ

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sophy, vol. i. part 2, second edition; and 'On the Secular Cooling of the Earth,' *Royal Society of Edinburgh*, 1862.

[1] 6th ed. 1872, p. 286.

and floræ, taken together, bear somewhat the same proportion to the whole series of living beings which have occupied this globe as the existing fauna and flora do to them.'

Herbert Spencer, in his article on 'Illogical Geology' in the 'Universal Review' for July 1859,[1] uses these words: 'Only the last chapter of the earth's history has come down to us. The many previous chapters, stretching back to a time immeasurably remote, have been burnt, and with them all the records of life we may presume they contained.' Indeed, so brief and unimportant does Herbert Spencer consider this last chapter to have been that he is puzzled to account for 'such evidences of progression as exist'; and finally concludes that they are of no significance in relation to the doctrine of evolution, but probably represent the succession of forms by which a newly upheaved land would be peopled. He argues that the earliest immigrants would be the lower forms of animal and vegetable life, and that these would be followed by an irregular succession of higher and higher forms, which 'would thus simulate the succession presented by our own sedimentary series.'

We see, then, what these three great writers on evolution thought on this subject: they were all convinced that the time during which the geologists concluded that the fossiliferous rocks had been formed was utterly insufficient to account for organic evolution.

Our object to-day is first to consider the objections raised by physicists against the time demanded by the geologist, and still more against its multiplication by the student of organic evolution; secondly, to inquire whether the present state of palæontological and zoological knowledge increases or diminishes the weight of the threefold opinion quoted above—an opinion formed on far more slender evidence than that which is now available. And if we find this opinion sustained, it must be considered to have a very important bearing upon the controversy.

The arguments of the physicists are three:—

First, the argument from the observed secular change in the length of the day the most important element of which is due to tidal retardation. It has been known for a very long time that the tides are slowly increasing the length of our day. Huxley explains the reason with his usual lucidity: 'That this must be so is obvious, if one considers, roughly, that the tides result from the pull which the sun and the moon exert upon the sea, causing it to act as a sort of break upon the solid earth.'[2]

A liquid earth takes a shape which follows from its rate of revolution, and from which, therefore, its rate of revolution can be calculated.

The liquid earth consolidated in the form it last assumed, and this shape has persisted until now, and informs us of the rate of revolution at the time of consolidation. Comparing this with the present rate, and knowing the amount of lengthening in a given time due to tidal friction, we can calculate the date of consolidation as certainly less than 1000 million years ago.

This argument is fallacious, as many mathematicians have shown. The present shape tells us nothing of the length of the day at the date of consolidation; for the earth, even when solid, will alter its form when exposed for a long time to the action of great forces. As Professor Perry said in a letter to Professor Tait:[3] 'I know that solid rock is not like cobbler's wax, but 1000 million years is a very long time, and the forces are great.' Furthermore, we know that the earth is always altering its shape, and that whole coast-lines are slowly rising or falling, and that this has been true, at any rate, during the formation of the stratified rocks.

This argument is dead and gone.[4] We are, indeed, tempted to wonder that the

[1] Reprinted in his *Essays*, 1868, vol. i. pp. 324–376.
[2] Anniv. Address to Geol. Soc. 1869.
[3] *Nature*, Jan. 3, 1895.
[4] It must not be forgotten, however, that this argument and those which follow it have done very good work in modifying the unreasonable demands of geologists a quarter of a century ago.

physicist, who was looking about for arguments by which to revise what he conceived to be the hasty conclusions of the geologist as to the age of the earth, should have exposed himself to such an obvious retort in basing his own conclusions as to its age on the assumption that the earth, which we know to be always changing in shape, has been unable to alter its equatorial radius by a few miles under the action of tremendous forces constantly tending to alter it, and having 1000 million years in which to do the work.

With this flaw in the case it is hardly necessary to insist on our great uncertainty as to the rate at which the tides are lengthening the day.

The spectacle presented by the geologist and biologist, deeply shocked at Lord Kelvin's extreme uniformitarianism in the domain of astronomy and cosmic physics, is altogether too comforting to be passed by without remark; but in thus indulging in a friendly *tu quoque*, I am quite sure that I am speaking for every member of this Section in saying that we are in no way behind the members of Section A in our pride and admiration at the noble work which he has done for science, and we are glad to take this opportunity of congratulating him on the half-century of work and teaching—both equally fruitful—which has reached its completion in the present year.

The second argument is based upon the cooling of the earth, and this is the one brought forward and explained by Lord Salisbury in his Presidential Address. It has been the argument on which perhaps the chief reliance has been placed, and of which the data—so it was believed—were the least open to doubt.

On the Sunday during the meeting of the British Association at Leeds (1890), I went for a walk with Professor Perry, and asked him to explain the physical reasons for limiting the age of the earth to a period which the students of other sciences considered to be very inadequate. He gave me an account of the data on which Lord Kelvin relied in constructing this second argument, and expressed the strong opinion that they were perfectly sound, while, as for the mathematics, it might be taken for granted, he said, that they were entirely correct. He did not attach much weight to the other arguments, which he regarded as merely offering support to the second.

This little piece of personal history is of interest, inasmuch as Professor Perry has now provided us with a satisfactory answer to the line of reasoning which so fully satisfied him in 1890. And he was led to a critical examination of the subject by the attitude taken up by Lord Salisbury in 1894. Professor Perry was not present at the meeting, but when he read the President's address, and saw how other conclusions were ruled out of court, how the only theory of evolution which commands anything approaching universal assent was set on one side because of certain assumptions as to the way in which the earth was believed to have cooled, he was seized with a desire to sift these assumptions, and to inquire whether they would bear the weight of such far-reaching conclusions. Before giving the results of his examination, it is necessary to give a brief account of the argument on which so much has been built.

Lord Kelvin assumed that the earth is a homogeneous mass of rock similar to that with which we are familiar on the surface. Assuming, further, that the temperature increases, on the average, 1° F. for every 50 feet of depth near the surface everywhere, he concluded that the earth would have occupied not less than twenty, nor more than four hundred, million years in reaching its present condition from the time when it first began to consolidate and possessed a uniform temperature of 7000° F.

If, in the statement of the argument, we substitute for the assumption of a homogeneous earth an earth which conducts heat better internally than it does toward the surface, Professor Perry, whose calculations have been verified by Mr. O. Heaviside, finds that the time of cooling has to be lengthened to an extent which depends upon the value assigned to the internal conducting power. If, for instance, we assume that the deeper part of the earth conducts ten times as well as the outer part, Lord Kelvin's age would require to be multiplied by fifty-six. Even if the conductivity be the same throughout, the increase of density in the

deeper part, by augmenting the capacity for heat of unit volume, implies a longer age than that conceded by Lord Kelvin. If the interior of the earth be fluid or contain fluid in a honeycomb structure, the rate at which heat can travel would be immensely increased by convection currents, and the age would have to be correspondingly lengthened. If, furthermore, such conditions, although not obtaining now, did obtain in past times, they will have operated in the same direction.

Professor Tait, in his letter to Professor Perry (published in 'Nature' of January 3, 1895), takes the entirely indefensible position that the latter is bound to prove the higher internal conductivity. The obligation is all on the other side, and rests with those who have pressed their conclusions hard and carried them far. These conclusions have been, as Darwin found them, one of our 'sorest troubles'; but when it is admitted that there is just as much to be said for another set of assumptions leading to entirely different conclusions, our troubles are at an end, and we cease to be terrified by an array of symbols, however unintelligible to us. It would seem that Professor Tait, without, as far as I can learn, publishing any independent calculation of the age of the earth, has lent the weight of his authority to a period of 10 million years, or half of Lord Kelvin's minimum. But in making this suggestion he apparently feels neither interest nor responsibility in establishing the data of the calculations which he borrowed to obtain therefrom a very different result from that obtained by their author.

Professor Perry's object was not to substitute a more correct age for that obtained by Lord Kelvin, but rather to show that the data from which the true age could be calculated are not really available. We obtain different results by making different assumptions, and there is no sufficient evidence for accepting one assumption rather than another. Nevertheless, there is some evidence which indicates that the interior of the earth in all probability conducts better than the surface. Its far higher density is consistent with the belief that it is rich in metals, free or combined. Professor Schuster concludes that the internal electric conductivity must be considerably greater than the external. Geologists have argued from the amount of folding to which the crust has been subjected that cooling must have taken place to a greater depth than 120 miles, as assumed in Lord Kelvin's argument. Professor Perry's assumption would involve cooling to a much greater depth.

Professor Perry's conclusion that the age of the habitable earth is lengthened by increased conductivity is the very reverse of that to which we should be led by a superficial examination of the case. Professor Tait, indeed, in the letter to which I have already alluded, has said: 'Why, then, drag in mathematics at all, since it is absolutely obvious that the better conductor the interior in comparison with the skin, the longer ago must it have been when the whole was at 7000 F., the state of the skin being as at present?' Professor Perry, in reply, pointed out that one mathematician who had refuted the tidal retardation argument [1] had assumed that the conditions described by Professor Tait would have involved a shorter period of time. And it is probable that Lord Kelvin thought the same; for he had assumed conditions which would give the result—so he believed at the time—most acceptable to the geologist and biologist. Professor Perry's conclusion is very far from obvious, and without the mathematical reasoning would not be arrived at by the vast majority of thinking men.

The 'natural man' without mathematics would say, so far from this being 'absolutely obvious,' it is quite clear that increased conductivity, favouring escape of heat, would lead to more rapid cooling, and would make Lord Kelvin's age even shorter.

The argument can, however, be put clearly without mathematics, and, with Professor Perry's help, I am able to state it in a few words. Lord Kelvin's assumption of an earth resembling the surface rock in its relations to heat leads to the present condition of things, namely, a surface gradient of 1° F. for every 50 feet, in 100,000,000 years, more or less. Deeper than 150 miles he imagines

[1] Rev. M. H. Close in *R. Dublin Soc.*, February 1878.

that there has been almost no cooling. If, however, we take one of the cases put by Professor Perry, and assume that below a depth of four miles there is ten times the conductivity, we find that after a period of 10,000,000,000 years the gradient at the surface is still 1° F. for every 50 feet; but that we have to descend to a depth of 1500 miles before we find the initial temperature of 7000° F. undiminished by cooling. In fact the earth, as a whole, has cooled far more quickly than under Lord Kelvin's conditions, the greater conductivity enabling a far larger amount of the internal heat to escape; but in escaping it has kept up the temperature gradient at the surface.

Lord Kelvin, replying to Professor Perry's criticisms, quite admits that the age at which he had arrived by the use of this argument may be insufficient. Thus, he says, in his letter [1]: 'I thought my range from 20 millions to 400 millions was probably wide enough, but it is quite possible that I should have put the superior limit a good deal higher, perhaps 4,000 instead of 400.'

The third argument was suggested by Helmholtz, and depends on the life of the sun. If the energy of the sun is due only to the mutual gravitation of its parts, and if the sun is now of uniform density, 'the amount of heat generated by his contraction to his present volume would have been sufficient to last 18 million years at his present rate of radiation.' [2] Lord Kelvin rejects the assumption of uniform density, and is, in consequence of this change, able to offer a much higher upward limit of 500 million years.

This argument also implies the strictest uniformitarianism as regards the sun. We know that other suns may suddenly gain a great accession of energy, so that their radiation is immensely increased. We only detect such changes when they are large and sudden, but they prepare us to believe that smaller accessions may be much more frequent, and perhaps a normal occurrence in the evolution of a sun. Such accessions may have followed from the convergence of a stream of meteors. Again, it is possible that the radiation of the sun may have been diminished and his energy conserved by a solar atmosphere.

Newcomb has objected to these two possible modes by which the life of the sun may have been greatly lengthened, that a lessening of the sun's heat by under a quarter would cause all the water on the earth to freeze, while an increase of much over half would probably boil it all away. But such changes in the amount of radiation received would follow from a greater distance from the sun of 15½ per cent., and a greater proximity to him of 18·4 per cent., respectively. Venus is inside the latter limit, and Mars outside the former, and yet it would be a very large assumption to conclude that all the water in the former is steam, and all in the latter ice. Indeed, the existence of water and the melting of snow on Mars are considered to be thoroughly well authenticated. It is further possible that in a time of lessened solar radiation the earth may have possessed an atmosphere which would retain a larger proportion of the sun's heat; and the internal heat of the earth itself, great lakes of lava under a canopy of cloud for example, may have played an important part in supplying warmth.

Again we have a greater age if there was more energy available than in Helmholtz's hypothesis. Lord Kelvin maintains that this is improbable because of the slow rotation of the sun, but Perry has given reasons for an opposite conclusion.

The collapse of the first argument of tidal retardation, and of the second of the cooling of the earth, warn us to beware of a conclusion founded on the assumption that the sun's energy depends, and has ever depended, on a single source of which we know the beginning and the end. It may be safely maintained that such a conclusion has not that degree of certainty which justifies the followers of one science in assuming that the conclusion of other sciences must be wrong, and in disregarding the evidence brought forward by workers in other lines of research.

We must freely admit that this third argument has not yet fully shared the fate

[1] *Nature*, January 3, 1895.

[2] Newcomb's *Popular Astronomy*, p. 523.

of the two other lines of reasoning. Indeed, Professor George Darwin, although not feeling the force of these latter, agrees with Lord Kelvin in regarding 500 million years as the maximum life of the sun.[1]

We may observe, too, that 500 million years is by no means to be despised: a great deal may happen in such a period of time. Although I should be very sorry to say that it is sufficient, it is a very different offer from Professor Tait's 10 million.

In drawing up this account of the physical arguments, I owe almost everything to Professor Perry for his articles in 'Nature' (January 3 and April 18, 1895), and his kindness in explaining any difficulties that arose. I have thought it right to enter into these arguments in some detail, and to consume a considerable proportion of our time in their discussion. This was imperatively necessary, because they claimed to stand as barriers across our path, and, so long as they were admitted to be impassable, any further progress was out of the question. What I hope has been an unbiassed examination has shown that, as barriers, they are more imposing than effective; and we are free to proceed, and to look for the conclusions warranted by our own evidence. In this matter we are at one with the geologists; for, as has been already pointed out, we rely on them for an estimate of the time occupied by the deposition of the stratified rocks, while they rely on us for a conclusion as to how far this period is sufficient for the whole of organic evolution.

First, then, we must briefly consider the geological argument, and I cannot do better than take the case as put by Sir Archibald Geikie in his Presidential Address to this Association at Edinburgh in 1892.

Arguing from the amount of material removed from the land by denuding agencies, and carried down to the sea by rivers, he showed that the time required to reduce the height of the land by one foot varies, according to the activity of the agencies at work, from 730 years to 6800 years. But this also supplies a measure of the rate of deposition of rock; for the same material is laid down elsewhere, and would of course add the same height of one foot to some other area equal in size to that from which it was removed.

The next datum to be obtained is the total thickness of the stratified rocks from the Cambrian system to the present day. 'On a reasonable computation these stratified masses, where most fully developed, attain a united thickness of not less than 100,000 feet. If they were all laid down at the most rapid recorded rate of denudation, they would require a period of seventy-three millions of years for their completion. If they were laid down at the slowest rate, they would demand a period of not less than 680 millions.'

The argument that geological agencies acted much more vigorously in past times he entirely refuted by pointing to the character of the deposits of which the stratified series is composed. 'We can see no proof whatever, nor even any evidence which suggests that on the whole the rate of waste and sedimentation was more rapid during Mesozoic and Palæozoic time than it is to-day. Had there been any marked difference in this rate from ancient to modern times, it would be incredible that no clear proof of it should have been recorded in the crust of the earth.'

It may therefore be inferred that the rate of deposition was no nearer the more rapid than the slower of the rates recorded above, and, if so, the stratified rocks would have been laid down in about 400 million years.

There are other arguments favouring the uniformity of conditions throughout the time during which the stratified rocks were laid down, in addition to those which are purely geological and depend upon the character of the rocks themselves. Although more biological than geological, these arguments are best considered here.

The geological agency to which attention is chiefly directed by those who desire to hurry up the phenomena of rock formation is that of the tides. But it seems

[1] *British Association Reports*, 1886, pp. 514–518.

certain that the tides were not sufficiently higher in Silurian times to prevent the deposition of certain beds of great thickness under conditions as tranquil as any of which we have evidence in the case of a formation extending over a large area. From the character of the organic remains it is known that these beds were laid down in the sea, and there are the strongest grounds for believing that they were accumulated along shores and in fairly shallow water. The remains of extremely delicate organisms are found in immense numbers, and over a very large area. The recent discovery, in the Silurian system of America, of trilobites, with their long delicate antennæ perfectly preserved, proves that in one locality (Rome, New York State) the tranquillity of deposition was quite as profound as in any locality yet discovered on this side of the Atlantic.

There are, then, among the older Palæozoic rocks a set of deposits than which we can imagine none better calculated to test the force of the tides; and we find that they supply evidence for exceptional tranquillity of conditions over a long period of time.

There is other evidence of the permanence, throughout the time during which the stratified rocks were deposited, of conditions not very dissimilar from those which obtain to-day. Thus the attachments of marine organisms, which are permanently rooted to the bottom or on the shores, did not differ in strength from those which we now find—an indication that the strains due to the movements of the sea did not greatly differ in the past.

We have evidence of a somewhat similar kind to prove uniformity in the movements of the air. The expanse of the wings of flying organisms certainly does not differ in a direction which indicates any greater violence in the atmospheric conditions. Before the birds had become dominant among the larger flying organisms, their place was taken by the flying reptiles, the pterodactyls, and before the appearance of these we know that, in Palæozoic times, the insects were of immense size, a dragon-fly from the Carboniferous rocks of France being upwards of 2 feet in the expanse of its wings. As one group after another of widely dissimilar organisms gained control of the air, each was in turn enabled to increase to the size which was best suited to such an environment, but we find that the limits which obtain to-day were not widely different in the past. And this is evidence for the uniformity in the strains due to wind and storm no less than to those due to gravity. Furthermore, the condition of the earth's surface at present shows us how extremely sensitive the flying organism is to an increase in the former of these strains, when it occurs in proximity to the sea. Thus it is well known that an unusually large proportion of the Madeiran beetles are wingless, while those which require the power of flight possess it in a stronger degree than on continental areas. This evolution in two directions is readily explained by the destruction by drowning of the winged individuals of the species which can manage to live without the power of flight, and of the less strongly winged individuals of those which need it. Species of the latter kind cannot live at all in the far more stormy Kerguelen Land, and the whole of the insect fauna is wingless.

The size and strength of the trunks of fossil trees afford, as Professor George Darwin has pointed out, evidence of uniformity in the strains due to the condition of the atmosphere.

We can trace the prints of raindrops at various geological horizons, and in some cases found in this country it is even said that the eastern side of the depressions is the more deeply pitted, proving that the rain drove from the west, as the great majority of our storms do to-day.

When, therefore, we are accused of uniformitarianism, as if it were an entirely unproved assumption, we can at any rate point to a large body of positive evidence which supports our contention, and the absence of any evidence against it. Furthermore, the data on which we rely are likely to increase largely, as the result of future work.

After this interpolation, chiefly of biological argument in support of the geologist, I cannot do better than bring the geological evidence to a close in the words which conclude Sir Archibald Geikie's address: 'After careful reflection on the subject, I affirm that the geological record furnishes a mass of evidence which no

arguments drawn from other departments of Nature can explain away, and which, it seems to me, cannot be satisfactorily interpreted save with an allowance of time much beyond the narrow limits which recent physical speculation would concede.'

In his letter to Professor Perry,[1] Lord Kelvin says:—

'So far as underground heat alone is concerned, you are quite right that my estimate was 100 million, and please remark [2] that that is all Geikie wants; but I should be exceedingly frightened to meet him now with only 20 million in my mouth.'

We have seen, however, that Geikie considered the rate of sedimentation to be, on the whole, uniform with that which now obtains, and this would demand a period of nearly 400 million years. He points out furthermore that the time must be greatly increased on account of the breaks and interruptions which occur in the series, so that we shall probably get as near an estimate as is possible from the data which are available by taking 450 million as the time during which the stratified rocks were formed.

Before leaving this part of the subject, I cannot refrain from suggesting a line of enquiry which may very possibly furnish important data for checking the estimates at present formed by geologists, and which, if the mechanical difficulties can be overcome, is certain to lead to results of the greatest interest and importance. Ever since the epoch-making voyage of the 'Challenger,' it has been known that the floor of the deep oceans outside the shallow shelf which fringes the continental areas is covered by a peculiar deposit formed entirely of meteoric and volcanic dust, the waste of floating pumice, and the hard parts of animals living in the ocean. Of these latter only the most resistant can escape the powerful solvent agencies. Many observations prove that the accumulation of this deposit is extremely slow. One indication of this is especially convincing: the teeth of sharks and the most resistant part of the skeleton—the ear-bones—of whales are so thickly spread over the surface that they are continually brought up in the dredge, while sometimes a single haul will yield a large number of them. Imagine the countless generations of sharks and whales which must have succeeded each other in order that these insignificant portions of them should be so thickly spread over that vast area which forms the ocean floor. We have no reason to suppose that sharks and whales die more frequently in the deep ocean than in the shallow fringing seas; in fact, many observations point in the opposite direction, for wounded and dying whales often enter shallow creeks and inlets, and not uncommonly become stranded. And yet these remains of sharks and whales, although well known in the stratified rocks which were laid down in comparatively shallow water and near coasts, are only found in certain beds, and then in far less abundance than in the oceanic deposit. We can only explain this difference by supposing that the latter accumulate with such almost infinite slowness as compared with the continental deposits that these remains form an important and conspicuous constituent of the one, while they are merely found here and there when looked for embedded in the other. The rate of accumulation of all other constituents is so slow as to leave a layer of teeth and ear-bones uncovered, or covered by so thin a deposit that the dredge can collect them freely. Dr. John Murray calculates that only a few inches of this deposit have accumulated since the Tertiary Period. These most interesting facts prove furthermore that the great ocean basins and continental areas have occupied the same relative positions since the formation of the first stratified rocks; for no oceanic deposits are found anywhere in the latter. We know the sources of the oceanic deposit, and it might be possible to form an estimate, within wide limits, of its rate of accumulation. If it were possible to ascertain its thickness by means of a boring, some conclusions as to the time which has elapsed during the lifetime of certain species—perhaps even the lifetime of the oceans themselves—might be arrived at. Lower down the remains of earlier species would probably be found. The depth of this deposit and its character at deeper levels are questions of overwhelming interest; and perhaps even more so is

[1] *Nature*, Jan. 3, 1895. [2] *P. L. and A.*, vol. ii. p. 87.

the question as to what lies beneath. Long before the 'Challenger' had proved the persistence of oceanic and continental areas, Darwin, with extraordinary foresight, and opposed by all other naturalists and geologists, including his revered teacher, Lyell, had come to the same conclusion. His reasoning on the subject is so convincing that it is remarkable that he made so few converts, and this is all the more surprising since the arguments were published in the 'Origin of Species,' which in other respects produced so profound an effect. In speculating as to the rocks in which the remains of the ancestors of the earliest known fossils may still exist, he suggested that, although the existing relationship between the positions of our present oceans and continental areas is of immense antiquity, there is no reason for the belief that it has persisted for an indefinite period, but that at some time long antecedent to the earliest known fossiliferous rocks 'continents may have existed where oceans are now spread out; and clear and open oceans may have existed where our continents now stand.' Not the least interesting result would be the test of this hypothesis, which would probably be forthcoming as the result of boring into the floor of a deep ocean; for although, as Darwin pointed out, it is likely enough that such rocks would be highly metamorphosed, yet it might still be possible to ascertain whether they had at any time formed part of a continental deposit, and perhaps to discover much more than this. Such an undertaking might be carried out in conjunction with other investigations of the highest interest, such as the attempt to obtain a record of the swing of a pendulum at the bottom of the ocean.

We now come to the strictly biological part of our subject—to the inquiry as to how much of the whole scheme of organic evolution has been worked out in the time during which the fossiliferous rocks were formed, and how far, therefore, the time required by the geologist is sufficient.

It is first necessary to consider Lord Kelvin's suggestion that life may have reached the earth on a meteorite—a suggestion which might be made the basis of an attempt to rescue us from the dilemma in which we were placed by the insufficiency of time for evolution. It might be argued that the evolution which took place elsewhere may have been merely completed, in a comparatively brief space of time, on our earth.

We know nothing of the origin of life here or elsewhere, and our only attitude towards this or any other hypothesis on the subject is that of the anxious inquirer for some particle of evidence. But a few brief considerations will show that no escape from the demands for time can be gained in this way.

Our argument does not deal with the time required for the origin of life, or for the development of the lowest beings with which we are acquainted from the first formed beings, of which we know nothing. Both these processes may have required an immensity of time; but as we know nothing whatever about them, and have as yet no prospect of acquiring any information, we are compelled to confine ourselves to as much of the process of evolution as we can infer from the structure of living and fossil forms—that is, as regards animals, to the development of the simplest into the most complex Protozoa, the evolution of the Metazoa from the Protozoa, and the branching of the former into its numerous Phyla, with all their Classes, Orders, Families, Genera, and Species. But we shall find that this is quite enough to necessitate a very large increase in the time estimated by the geologist.

The Protozoa, simple and complex, still exist upon the earth in countless species, together with the Metazoan Phyla. Descendants of forms which in their day constituted the beginning of that scheme of evolution which I have defined above, descendants, furthermore, of a large proportion of those forms which, age after age, constituted the shifting phases of its onward progress, still exist, and in a sufficiently unmodified condition to enable us to reconstruct, at any rate in mere outline, the history of the past. Innumerable details and many phases of supreme importance are still hidden from us, some of them perhaps never to be recovered. But this frank admission, and the eager and premature attempts to expound too much, to go further than the evidence permits, must not be allowed

to throw an undeserved suspicion upon conclusions which are sound and well supported, upon the firm conviction of every zoologist that the general trend of evolution has been, as I have stated it, that each of the Metazoan Phyla originated, directly or indirectly, in the Protozoa.

The argument founded on the meteorite hypothesis would, however, require that the process of evolution went backward on a scale as vast as that on which it went forward, that certain descendants of some central type, coming to the earth on a meteorite, gradually lost their Metazoan complexity and developed backward into the Protozoa, throwing off the lower Metazoan Phyla on the way, while certain other descendants evolved all the higher Metazoan groups. Such a process would shorten the period of evolution by half, but it need hardly be said that all available evidence is entirely against it.

The only other assumption by means of which the meteorite hypothesis might be used to shorten the time is even more wild and improbable. Thus it might be supposed that the evolution which we believe to have taken place on this earth, really took place elsewhere—at any rate as regards all its main lines—and that samples of all the various phases, including the earliest and simplest, reached us by a regular meteoric service, which was established at some time after the completion of the scheme of organic evolution. Hence the evidences which we study would point to an evolution which occurred in some unknown world with an age which even Professor Tait has no desire to limit.

If these wild assumptions be rejected, there remains the supposition that, if life was brought by a meteorite, it was life no higher than that of the simplest Protozoon—a supposition which leaves our argument intact. The alternative supposition, that one or more of the Metazoan Phyla were introduced in this way while the others were evolved from the terrestrial Protozoa, is hardly worth consideration. In the first place, some evidence of a part in a common scheme of evolution is to be found in every Phylum. In the second place, the gain would be small; the arbitrary assumption would only affect the evidence of the time required for evolution derived from the particular Phylum or Phyla of supposed meteoric origin.

The meteoric hypothesis, then, can only affect our argument by making the most improbable assumptions, for which, moreover, not a particle of evidence can be brought forward.

We are therefore free to follow the biological evidence fearlessly. It is necessary, in the first place, to expand somewhat the brief outline of the past history of the animal kingdom, which has already been given. Since the appearance of the 'Origin of Species,' the zoologist, in making his classifications, has attempted as far as possible to set forth a genealogical arrangement. Our purpose will be served by an account of the main outlines of a recent classification, which has been framed with a due consideration for all sides of zoological research, new and old, and which has met with general approval. Professor Lankester divides the animal kingdom into two grades, the higher of which, the Enterozoa (Metazoa), were derived from the lower, the Plastidozoa (Protozoa). Each of these grades is again divided into two sub-grades, and each of these is again divided into Phyla, corresponding more or less to the older Sub-Kingdoms. Beginning from below, the most primitive animals in existence are found in the seven Phyla of the lower Protozoan sub-grade, the Gymnomyxa. Of these unfortunately only two, the Reticularia (Foraminifera) and Radiolaria, possess a structure which renders possible their preservation in the rocks. The lowest and simplest of these Gymnomyxa represent the starting-point of that scheme of organic evolution which we are considering to-day. The higher order of Protozoan life, the sub-grade Corticata, contains three Phyla, no one of which is available in the fossil state. They are, however, of great interest and importance to us as showing that the Protozoan type assumes a far higher organisation on its way to evolve the more advanced grade of animal life. The first-formed of these latter are contained in the two Phyla of the sub-grade Cœlentera, the Porifera or Sponges, and the Nematophora or Corals, Sea-Anemones, Hydrozoa and allied groups. Both of these Phyla are plentifully represented in the fossil state. It is considered certain that the latter of these, the Nematophora,

gave rise to the higher sub-grade, the Cœlomata, or animals with a cœlom or body-cavity surrounding the digestive tract. This latter includes all the remaining species of animals in nine Phyla, five of which are found fossil—the Echinoderma, Gephyrea, Mollusca, Appendiculata, and Vertebrata.

Before proceeding further, I wish to lay emphasis on the immense evolutionary history which must have been passed through before the ancestor of one of the higher of these nine Phyla came into being. Let us consider one or two examples, since the establishment of this position is of the utmost importance for our argument. First, consider the past history of the Vertebrata,—of the common ancestor of our Balanoglossus, Tunicates, Amphioxus, Lampreys, Fishes, Dipnoi, Amphibia, Reptiles, Birds, and Mammals. Although zoologists differ very widely in their opinions as to the affinities of this ancestral form, they all agree in maintaining that it did not arise direct from the Nematophora in the lower sub-grade of Metazoa, but that it was the product of a long history within the Cœlomate subgrade. The question as to which of the other Cœlomate Phyla it was associated with will form the subject of one of our discussions at this meeting; and I will therefore say no more upon this period of its evolution, except to point out that the very question itself, 'the ancestry of Vertebrates,' only means a relatively small part of the evolutionary history of the Vertebrate ancestor within the Cœlomate group. For when we have decided the question of the other Cœlomate Phylum or Phyla to which the ancestral Vertebrate belonged, there remains of course the history of that Phylum or those Phyla earlier than the point at which the Vertebrate diverged, right back to the origin of the Cœlomata; while, beyond and below, the wide gulf between this and the Cœlentera had to be crossed, and then, probably after a long history as a Cœlenterate, the widest and most significant of all the morphological intervals—that between the lowest Metazoon and the highest Protozoon—was traversed. But this was by no means all. There remains the history within the higher Protozoan sub-grade, in the interval from this to the lower, and within the lower sub-grade itself, until we finally retrace our steps to the lowest and simplest forms. It is impossible to suppose that all this history of change can have been otherwise than immensely prolonged; for it will be shown below that all the available evidence warrants the belief that the changes during these earlier phases were at least as slow as those which occurred later.

If we take the history of another of the higher Phyla, the Appendiculata, we find that the evidence points in the same direction. The common ancestor of our Rotifera, earthworms, leeches, Peripatus, centipedes, insects, Crustacea, spiders and scorpions, and forms allied to all these, is generally admitted to have been Chætopod-like, and probably arose in relation to the beginnings of certain other Cœlomata Phyla, such as the Gephyrea and perhaps Mollusca. At the origin of the Cœlomate sub-grade the common ancestor of all Cœlomate Phyla is reached, and its evolution has been already traced in the case of the Vertebrata.

What is likely to be the relation between the time required for the evolution of the ancestor of a Cœlomate Phylum and that required for the evolution, which subsequently occurred, within the Phylum itself? The only indication of an answer to this question is to be found in a study of the rate of evolution in the lower parts of the animal kingdom as compared with that in the higher. Contrary, perhaps, to anticipation, we find that all the evidences of rapid evolution are confined to the most advanced of the smaller groups within the highest Phyla, and especially to the higher Classes of the Vertebrata. Such evidence as we have strongly indicates the most remarkable persistence of the lower animal types. Thus in the Class Imperforata of the Reticularia (Foraminifera) one of our existing genera (Saccamina) occurs in the Carboniferous strata, another (Trochammina) in the Permian, while a single new genus (Receptaculites) occurs in the Silurian and Devonian. The evidence from the Class Perforata is much stronger, the existing genera Nodosaria, Dentalina, Textularia, Grammostomum, Valvulina, and Nummulina all occurring in the Carboniferous, together with the new genera Archædiscus (?) and Fusulina.

I omit reference to the much-disputed Eozoon from the Laurentian rocks far

below the horizon, which for the purpose of this address I am considering as the lowest fossiliferous stratum. We are looking forward to the new light which will be thrown upon this form in the communication of its veteran defender, Sir William Dawson, whom we are all glad to welcome.

Passing the Radiolaria, with delicate skeletons less suited for fossilisation, and largely pelagic and therefore less likely to reach the strata laid down along the fringes of the continental areas, the next Phylum which is found in a fossil state is that of the Porifera, including the sponges, and divided into two Classes, the Calcispongiæ and Silicospongiæ. Although the fossilisation of sponges is in many cases very incomplete, distinctly recognisable traces can be made out in a large number of strata. From these we know that representatives of all the groups of both Classes (except the Halisarcidæ, which have no hard parts) occurred in the Silurian, Devonian, and Carboniferous systems. The whole Phylum is an example of long persistence with extremely little change. And the same is true of the Nematophora: new groups indeed come in, sometimes extremely rich in species, such as the Palæozoic Rugose corals and Graptolites; but they existed side by side with representatives of existing groups, and they are not in themselves primitive or ancestral. A study of the immensely numerous fossil corals reveals no advance in organisation, while researches into the structure of existing Alcyonaria and Hydrocorallina have led to the interpretation of certain Palæozoic forms which were previously obscure, and the conclusion that they find their place close beside the living species.

All available evidence points to the extreme slowness of progressive evolutionary changes in the Cœlenterate Phyla, although the Protozoa, if we may judge by the Reticularia (Foraminifera), are even more conservative.

When we consider later on the five Cœlomate Phyla which occur fossil, we shall find that the progressive changes were slower and indeed hardly appreciable in the two lower and less complex Phyla, viz.: the Echinoderma, and Gephyrea, as compared with the Mollusca, Appendiculata, and Vertebrata.

Within these latter Phyla we have evidence for the evolution of higher groups presenting a more or less marked advance in organisation. And not only is the rate of development more rapid in the highest Phyla of the animal kingdom, but it appears to be most rapid when dealing with the highest animal tissue, the central nervous system. The chief, and doubtless the most significant, difference between the early Tertiary mammals and those which succeeded them, between the Secondary and Tertiary reptiles, between man and the mammals most nearly allied to him, is a difference in the size of the brain. In all these cases an enormous increase in this, the dominant tissue of the body, has taken place in a time which, geologically speaking, is very brief.

When glancing later on over the evolution which has taken place within the Phyla, further details upon this subject will be given, although in this as in other cases the time at our disposal demands that the exposition of evidence must largely yield to an exposition of the conclusions which follow from its study. And undoubtedly a study of all the available evidence points to the conclusion that in the lower grade, sub-grades, and Phyla of the animal kingdom evolution has been extremely slow as compared with that in the higher. We do not know the reason. It may be that this remarkable persistence through the stratified series of deposits is due to an innate fixity of constitution which has rigidly limited the power of variation; or, more probably perhaps, that the lower members of the animal kingdom were, as they are now, more closely confined to particular environments, with particular sets of conditions, with which they had to cope, and, this being successfully accomplished, natural selection has done little more than keep up a standard of organisation which was sufficient for their needs; while the higher and more aggressive forms ranging over many environments, and always prone to encounter new sets of conditions, were compelled to undergo responsive changes or to succumb. But whatever be the cause, the fact remains, and is of importance for our argument. When the ancestor of one of the higher Phyla was associated with the lower Phyla of the Cœlomate sub-grade, when further back it passed through a Cœlenterate, a higher Protozoan, and finally a lower

Protozoan phase, we are led to believe that its evolution was probably very slow as compared with the rate which it subsequently attained. But this conclusion is of the utmost importance; for the history contained in the stratified rocks nowhere reveals to us the origin of a Phylum. And this is not mere negative evidence, but positive evidence of the most unmistakable character. All the five Cœlomate Phyla which occur fossil appear low down in the Palæozoic rocks, in the Silurian or Cambrian strata, and they are represented by forms which are very far from being primitive, or, if primitive, are persistent types, such as Chiton, which are now living. Thus Vertebrata are represented by fishes, both sharks and ganoids; the Appendiculata by cockroaches, scorpions, Limulids, Trilobites, and many Crustacea; the Mollusca by Nautilus and numerous allied genera, by Dentalium, Chiton, Pteropods, and many Gastropods and Lamellibranchs; the Gephyrea by very numerous Brachiopods, and many Polyzoa; the Echinoderma by Crinoids, Cystoids, Blastoids, Asteroids, Ophiuroids, and Echinoids. It is just conceivable, although, as I believe, most improbable, that the Vertebrate Phylum originated at the time when the earliest known fossiliferous rocks were laid down. It must be remembered, however, that an enormous morphological interval separates the fishes which appear in the Silurian strata from the lower branches, grades, and classes of the Phylum in which Balanoglossus, the Ascidians, Amphioxus, and the Lampreys are placed. The earliest Vertebrates to appear are, in fact, very advanced members of the Phylum, and, from the point of view of anatomy, much nearer to man than to Amphioxus. If, however, we grant the improbable contention that so highly organised an animal as a shark could be evolved from the ancestral vertebrate in the period which intervened between the earliest Cambrian strata and the Upper Silurian, it is quite impossible to urge the same with regard to the other Phyla. It has been shown above that when these appear in the Cambrian and Silurian, they are flourishing in full force, while their numerous specialised forms are a positive proof of a long antecedent history within the limits of the Phylum.

If, however, we assume for the moment that the Phyla began in the Cambrian, the geologist's estimate must still be increased considerably, and perhaps doubled, in order to account for the evolution of the higher Phyla from forms as low as many which are now known upon the earth; unless, indeed, it is supposed, against the weight of all such evidence as is available, that the evolutionary history in these early times was comparatively rapid.

To recapitulate, if we represent the history of animal evolution by the form of a tree, we find that the following growth took place in some age antecedent to the earliest fossil records, before the establishment of the higher Phyla of the Animal Kingdom. The main trunk representing the lower Protozoa divided, originating the higher Protozoa; the latter portion again divided, probably in a threefold manner, originating the two lowest Metazoan Phyla, constituting the Cœlentera. The branch representing the higher of these Phyla, the Nematophora, divided, originating the lower Cœlomate Phyla, which again branched and originated the higher Phyla. And, as has been shown above, the relatively ancestral line, at every stage of this complex history, after originating some higher line, itself continued down to the present day, throughout the whole series of fossiliferous rocks, with but little change in its general characters, and practically nothing in the way of progressive evolution. Evidences of marked advance are to be found alone in the most advanced groups of the latest highest products—the Phyla formed by the last of these divisions.

It may be asked how is it possible for the zoologist to feel so confident as to the past history of the various animal groups. I have already explained that he does not feel this confidence as regards the details of the history, but as to its general lines. The evidence which leads to this conviction is based upon the fact that animal structure and mode of development can be, and have been, handed down from generation to generation from a period far more remote than that which is represented by the earliest fossils; that fundamental facts in structure and development may remain changeless amid endless changes of a more general character; that especially favourable conditions have preserved

ancestral forms comparatively unchanged. Working upon this material, comparative anatomy and embryology can reconstruct for us the general aspects of a history which took place long before the Cambrian rocks were deposited. This line of reasoning may appear very speculative and unsound, and it may easily become so when pressed too far. But applied with due caution and reserve, it may be trusted to supply us with an immense amount of valuable information which cannot be obtained in any other way. Furthermore, it is capable of standing the very true and searching test supplied by the verification of predictions made on its authority. Many facts taken together lead the zoologist to believe that A was descended from C through B; but if this be true, B should possess certain characters which are not known to belong to it. Under the inspiration of hypothesis a more searching investigation is made, and the characters are found. Again, that relatively small amount of the whole scheme of animal evolution which is contained in the fossiliferous rocks has furnished abundant confirmation of the validity of the zoologist's method. The comparative anatomy of the higher Vertebrate Classes leads the zoologist to believe that the toothless beak and the fused caudal vertebræ of a bird were not ancestral characters, but were at some time derived from a condition more conformable to the general plan of vertebrate construction, and especially to that of reptiles. Numerous secondary fossils prove to us that the birds of that time possessed teeth and separate caudal vertebræ, culminating in the long lizard-like tail of Archæopteryx.

Prediction and confirmation of this kind, both zoological and palæontological, have been going on ever since the historic point of view was adopted by the naturalist as the outcome of Darwin's teaching, and the zoologist may safely claim that his method, confirmed by palæontology so far as evidence is available, may be extended beyond the period in which such evidence is to be found.

And now our last endeavour must be to obtain some conception of the amount of evolution which has taken place within the higher Phyla of the Animal Kingdom during the period in which the fossiliferous rocks were deposited. The evidence must necessarily be considered very briefly, and we shall be compelled to omit the Vertebrata altogether.

The Phylum Appendiculata is divided by Lankester into three branches, the first containing the Rotifera, the second the Chætopoda, the third the Arthropoda. Of these the second is the oldest, and gave rise to the other two, or at any rate to the Arthropoda, with which we are alone concerned, inasmuch as the fossil records of the others are insufficient. The Arthropoda contain seven Classes, divided into two grades, according to the presence or absence of antennæ—the Ceratophora, containing the Peripatoidea, the Myriapoda, and the Hexapoda (or insects); the Acerata, containing the Crustacea, Arachnida, and two other classes (the Pantopoda and Tardigrada) which we need not consider. The first Class of the antenna-bearing group contains the single genus Peripatus—one of the most interesting and ancestral of animals, as proved by its structure and development, and by its immense geographical range. Ever since the researches of Moseley and Balfour, extended more recently by those of Sedgwick, it has been recognised as one of the most beautiful of the connecting links to be found amongst animals, uniting the antenna-bearing Arthropods, of which it is the oldest member, with the Chætopods. Peripatus is a magnificent example of the far-reaching conclusions of zoology, and of its superiority to palæontology as a guide in unravelling the tangled history of animal evolution. Peripatus is alive to-day, and can be studied in all the details of its structure and development; it is infinitely more ancestral, and tells of a far more remote past than any fossil Arthropod, although such fossils are well known in all the older of the Palæozoic rocks. And yet Peripatus is not known as a fossil. Peripatus has come down, with but little change, from a time, on a moderate estimate, at least twice as remote, and probably many times as remote, as the earliest known Cambrian fossil. The agencies which, it is believed, have crushed and heated the Archæan rocks so as to obliterate the traces of life which they contained were powerless to efface this ancient type, for, although the passing generations may have escaped record, the likeness of each was stamped on that

which succeeded it, and has continued down to the present day. It is, of course, a perfectly trite and obvious conclusion but not the less one to be wondered at, that the force of heredity should thus far outlast the ebb and flow of terrestrial change throughout the vast period over which the geologist is our guide.

If, however, the older Palæozoic rocks tell us nothing of the origin of the antenna-bearing Arthropods, what do they tell us of the history of the Myriapod and Hexapod Classes?

The Myriapods are well represented in Palæozoic strata, two species being found in the Devonian and no less than thirty-two in the Carboniferous. Although placed in an Order (Archipolypoda) separate from those of living Myriapods, these species are by no means primitive, and do not supply any information as to the steps by which the Class arose. The imperfection of the record is well seen in the traces of this Class; for between the Carboniferous rocks and the Oligocene there are no remains of undoubted Myriapods.

We now come to the consideration of insects, of which an adequate discussion would occupy a great deal too much of your time. An immense number of species are found in the Palæozoic rocks, and these are considered by Scudder, the great authority on fossil insects, to form an Order, the Palæodictyoptera, distinct from any of the existing Orders. The latter, he believes, were evolved from the former in Mesozoic times. These views do not appear to derive support from the wonderful discoveries of M. Brongniart [1] in the Upper Carboniferous of Commentry in the Department of Allier in Central France. Concerning this marvellous assemblage of species, arranged by their discoverer into 46 genera and 101 species, Scudder truly says:

'Our knowledge of Palæozoic insects will have been increased three or four fold at a single stroke. . . . . No former contribution in this field can in any way compare with it, nor even all former contributions taken together.' [2]

When we remember that the group of fossil insects, of which so much can be affirmed by so great an authority as Scudder, lived at one time and in a single locality, we cannot escape the conclusion that the insect fauna of the habitable earth during the whole Palæozoic period was of immense importance and variety. Our knowledge of this single group of species is largely due to the accident that coal-mining in Commentry is carried on in the open air.

Now, these abundant remains of insects, so far from upholding the view that the existing orders had not been developed in Palæozoic times, are all arranged by Brongniart in four out of the nine Orders into which insects are usually divided, viz. the Orthoptera, Neuroptera, Thysanoptera, and Homoptera. The importance of the discovery is well seen in the Neuroptera, the whole known Palæozoic fauna of this Order being divided into 45 genera and 99 species, of which 33 and 72 respectively have been found at Commentry.

Although the Carboniferous insects of Commentry are placed in new families, some of them come wonderfully near those into which existing insects are classified, and obviously form the precursors of these. This is true of the Blattidæ, Phasmidæ, Acridiidæ, and Locustidæ among the Orthoptera, the Perlidæ among the Neuroptera, and the Fulgoridæ among the Homoptera. The differences which separate these existing families from their Carboniferous ancestors are most interesting and instructive. Thus the Carboniferous cockroaches possessed ovipositors, and probably laid their eggs one at a time, while ours are either viviparous or lay their eggs in a capsule. The Protophasmidæ resemble living species in the form of the head, antennæ, legs, and body; but while our species are either wingless or, with the exception of the female Phyllidæ, have the anterior pair reduced to tegmina, useless for flight, those of Palæozoic times possessed four well-developed wings. The forms representing locusts and grasshoppers (Palæacridiidæ) possessed long slender antennæ like the green grasshoppers (Locustidæ), from which the Acridiidæ are now distinguished by their short antennæ. The divergence and specialisation which is thus shown is amazingly small in amount. In

[1] Charles Brongniart.—'Recherches pour servir à l'Histoire des Insectes fossiles des temps primaires, précédées d'une Etude sur la nervation des ailes des Insectes.' 1894. [2] S. H. Scudder, *Am. Journ. Sci.*, vol. xlvii. February 1894. Art. viii.

the vast period between the Upper Carboniferous rocks and the present day the cockroaches have gained a rather different wing venation, and have succeeded in laying their eggs in a manner rather more specialised than that of insects in general; the stick insects and leaf insects have lost or reduced their wings, the grasshoppers have shortened their antennæ. These, however, are the insects which most closely resemble the existing species; let us turn to the forms which exhibit the greatest differences. Many species have retained in the adult state characters which are now confined to the larval stage of existence, such as the presence of tracheal gills on the sides of the abdomen. In some, the two membranes of the wing were not firmly fixed together, so that the blood could circulate freely between them. On the other hand, they are not very firmly fixed together in existing insects. Another important point was the condition of the three thoracic segments, which were quite distinct and separate, instead of being fused as they are now in the imago stage. This external difference probably also extended to the nervous system, so that the thoracic ganglia were separate instead of concentrated. The most interesting distinction, however, was the possession by many species of a pair of prothoracic appendages much resembling miniature wings, and which especially suggest the appearance assumed by the anterior pair (tegmina) in existing Phasmidæ. There is some evidence in favour of the view that they were articulated, and they exhibit what appears to be a trace of venation. Brongniart concludes that in still earlier strata, insects with six wings will be discovered, or rather insects with six of the tracheal gills sufficiently developed to serve as parachutes. Of these, the two posterior pair developed into the wings as we know them, while the anterior pair degenerated, some of the Carboniferous insects presenting us with a stage in which degeneration had taken place but was not complete.

One very important character was, as I have already pointed out, the enormous size reached by insects in this distant period. This was true of the whole known fauna as compared with existing species, but it was especially the case with the Protodonata, some of these giant dragon-flies measuring over two feet in the expanse of the wings.

As regards the habits of life and metamorphoses, Brongniart concludes that some species of Protoephemeridæ, Protoperlidæ, &c., obtained their food in an aquatic larval stage, and did not require it when mature. He concludes that the Protodonata fed on other animals, like our dragon-flies; that the Palæacridiidæ were herbivorous like our locusts and grasshoppers. the Protolocustidæ herbivorous and animal feeders like our green grasshoppers, the Palæoblattidæ omnivorous like our cockroaches. The Homoptera, too, had elongated sucking mouth-parts like the existing species. It is known that in Carboniferous times there was a lake with rivers entering it, at Commentry. From their great resemblance to living forms of known habits, it is probable that the majority of these insects lived near the water and their larvæ in it.

When we look at this most important piece of research as a whole, we cannot fail to be struck with the small advance in insect structure which has taken place since Carboniferous times. All the great questions of metamorphosis, and of the structures peculiar to insects, appear to have been very much in the position in which they are to-day. It is indeed probable enough that the Orders which zoologists have always recognised as comparatively modern and specialised, such as the Lepidoptera, Coleoptera, and Hymenoptera, had not come into existence. But as regards the emergence of the Class from a single primitive group, as regards its approximation towards the Myriapods, which lived at the same time, and of both towards their ancestor Peripatus, we learn absolutely nothing. All we can say is that there is evidence for the evolution of the most modern and specialised members of the Class, and some slight progressive evolution in the rest. Such evolution is of importance as giving us some vague conception of the rate at which the process travels in this division of the Arthropoda. If we look upon development as a series of paths which, by successively uniting, at length meet in a common point, then some conception of the position of that distant centre may be gained by measuring the angle of divergence and finding the number of unions which occur in a given length. In this case, the amount of approximation and union shown in

the interval between the Carboniferous Period and the present day is relatively so small that it would require to be multiplied many times before we could expect the lines to meet in the common point, the ancestor of insects, to say nothing of the far more distant past, in which the Tracheate Arthropods met in an ancestor presenting many resemblances to Peripatus. But it must not be forgotten that all this vast undefined period is required for the history of one of the two grades of one of the three branches of the whole Phylum.

Turning now to the brief consideration of the second grade of Arthropods, distinguished from the first grade by the absence of antennæ, the Trilobites are probably the nearest approach to an ancestral form met with in the fossil state. Now that the possession of true antennæ is certain, it is reasonable to suppose that the Trilobites represent an early Class of the Aceratous branch which had not yet become Aceratous. They are thus of the deepest interest in helping us to understand the origin of the antennaless branch, not by the ancestral absence, but by the loss of true antennæ which formerly existed in the group. But the Trilobites did not themselves originate the other Classes, at any rate during Palæozoic times. They represent a large and dominant Class, presenting more of the characters of the common ancestor than the other Classes; but the latter had diverged and had become distinct long before the earliest fossiliferous rocks; for we find well-marked representatives of the Crustacea in Cambrian, and of the Arachnida in Silurian strata. The Trilobites, moreover, appear in the Cambrian with many distinct and very different forms, contained in upwards of forty genera, so that we are clearly very far from the origin of the group.

Of the lower group of Crustacea, the Entomostraca, the Cirripedes are represented by two genera in the Silurian, the Ostracodes by four genera in the Cambrian and over twenty in the Silurian; of these latter, two genera (Cythere and Bairdia) continue right through the fossiliferous series and exist at the present day. Remains of Phyllopods are more scanty, but can be traced in the Devonian and Carboniferous rocks. The early appearance of the Cirripedes is of especial interest, inasmuch as the fixed condition of these forms in the mature state is certainly not primitive, and yet, nevertheless, appears in the earliest representatives.

The higher group, the Malacostraca, are represented by many genera of Phyllocarida in the Silurian and Devonian, and two in the Cambrian. These also afford a good example of the imperfection of the record, inasmuch as no traces of the group are to be found between the Carboniferous and our existing fauna in which it is represented by the genus Nebalia. The Phyllocarida are recognised as the ancestors of the higher Malacostraca, and yet these latter already existed—in small numbers, it is true—side by side with the Phyllocarida in the Devonian. The evolution of the one into the other must have been much earlier. Here, as in the Arthropoda, we have evidence of progressive evolution among the highest groups of the Class, as we see in the comparatively late development of the Brachyura as compared with the Macrura. We find no trace of the origin of the Class, or of the larger groups into which it is divided, or, indeed, of the older among the small groupings into families and genera.[1]

Of the Arachnida, although some of the most wonderful examples of persistent types are to be found in this class, but little can be said. Merely to state the bare fact that three kinds of scorpion are found in the Silurian, two Pedipalpi, eight scorpions, and two spiders in the Carboniferous, is sufficient to show that the period computed by geologists must be immensely extended to account for the development of this Class alone, inasmuch as it existed in a highly specialised condition almost at the beginning of the fossiliferous series; while, as regards so extraordinarily complex an animal as a scorpion, nothing apparent in the way of progressive development has happened since. Professor Lankester has, however, pointed out to me that the Silurian scorpion Palæophonus possessed heavier limbs than those of existing species, and this is a point in favour of an aquatic life like that of its near relation, Limulus. If so, it is probable that it possessed external

[1] For an account of the evolution of the Crustacea see the Presidential Addresses to the Geological Society in 1895 and 1896 by Dr. Henry Woodward.

gills, not yet inverted to form the lung-book. The Merostomata are of course a Palæozoic group, and reach their highest known development at their first appearance in the Silurian; since then they have done nothing but disappear gradually, leaving the single genus Limulus, unmodified since its first appearance in the Trias, to represent them. It is impossible to find clearer evidence of the decline rather than the rise of a group. No progressive development, but a gradual or rapid extinction, and consequent reduction in the number of genera and species, is a summary of the record of the fossiliferous rocks as regards this group and many others, such as the Trilobites, the Brachiopods, and the Nautilidæ. All these groups begin with many forms in the oldest fossiliferous rocks, and three of them have left genera practically unchanged from their first appearance to the present day. What must have been the time required to carry through the vast amount of structural change implied in the origin of these persistent types and the groups to which they belong—a period so extended that the interval between the oldest Palæozoic rocks and the present day supplies no measurable unit?

But I am digressing from the Appendiculate Phylum. We have seen that the fossil record is unusually complete as regards two Classes in each grade of the Arthropod branch, but that these Classes were well developed and flourishing in Palæozoic times. The only evidence of progressive evolution is in the development of the highest orders and families of the Classes. Of the origin of the Classes nothing is told, and we can hardly escape the conclusion that for the development of the Arthropod branches from a common Chætopod-like ancestor, and for the further development of the Classes of each branch, a period many times the length of the fossiliferous series is required, judging from the insignificant amount of development which has taken place during the formation of this series.

It is impossible to consider the other Cœlomate Phyla as I have done the Appendiculata. I can only briefly state the conclusions to which we are led.

As regards the Molluscan Phylum, the evidence is perhaps even stronger than in the Appendiculata. Representatives of the whole of the Classes are, it is believed, found in the Cambrian or Lower Silurian. The Pteropods are generally admitted to be a recent modification of the Gastropods, and yet, if the fossils described in the genera Conularia, Hyolithes, Pterotheca, &c. are true Pteropods, as they are supposed to be, they occur in the Cambrian and Silurian strata, while the group of Gastropods from which they almost certainly arose, the Bullidæ, are not known before the Trias. Furthermore, the forms which are clearly the oldest of the Pteropods—Limacina and Spirialis—are not known before the beginning of the Tertiary Period. Either there is a mistake in the identification of the Palæozoic fossils as Pteropods, or the record is even more incomplete than usual, and the most specialised of all Molluscan groups had been formed before the date of the earliest fossiliferous rocks. Even if this should hereafter be disproved, there can be no doubt about the early appearance of the Molluscan Classes, and that it is the irony of an incomplete record which places the Cephalopods and Gastropods in the Cambrian and the far more ancestral Chiton no lower than the Silurian. Throughout the fossiliferous series the older families of Gastropods and Lamellibranchs are followed by numerous other families, which were doubtless derived from them; new and higher groups of Cephalopods were developed, and, with the older groups, either persisted until the present time or became extinct. But in all this splitting up of the Classes into groups of not widely different morphological value, there is very little progressive modification, and, taking such changes in such a period as our unit for the determination of the time which was necessary for the origin of the Classes from a form like Chiton, we are led to the same conclusion as that which followed from the consideration of the Appendiculata, viz. that the fossiliferous series would have to be multiplied several times in order to provide it.

Of the Phylum Gephyrea, I will only mention the Brachiopods, which are found in immense profusion in the early Palæozoic rocks and which have occupied the subsequent time in becoming less dominant and important. So far from helping us to clear up the mystery which surrounds the origin of the Class, the earliest forms are quite as specialised as those living now, and, some of them (Lingula,

Discina) even generically identical. The demand for time to originate the group is quite as grasping as that of the others we have been considering.

All the Classes of Echinoderma, except the Holothurians, which do not possess a structure favourable for fossilisation, are found early in the Palæozoic rocks, and many of them in the Cambrian. Although these early forms are very different from those which succeeded them in the later geological periods, they do not possess a structure which can be recognised as in any way primitive or ancestral. The Echinoderma are the most distinct and separate of all the Cœlomate Phyla, and they were apparently equally distinct and separate at the beginning of the fossiliferous series.

In concluding this imperfect attempt to deal with a very vast subject in a very short time, I will remind you that we were led to conclude that the evolution of the ancestor of each of the higher animal Phyla probably occupied a very long period, perhaps as long as that required for the evolution which subsequently occurred within the Phylum. But the consideration of the higher Phyla which occur fossil, except the Vertebrata, leads to the irresistible conclusion that the whole period in which the fossiliferous rocks were laid down must be multiplied several times for this later history alone. The period thus obtained requires to be again increased, and perhaps doubled, for the earlier history.

In the preparation of the latter part of this address I have largely consulted Zittel's great work. I wish also to express my thanks to my friend Professor Lankester, whom I have consulted on many of the details, as well as the general plan which has been adopted.

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THEORIES OF EVOLUTION.

BY EDWARD B. POULTON.[1]

In dealing with theories of evolution, I think that we shall all be agreed that we may leave out of consideration the question of the origin of life, and deal only with what has happened to life after its appearance, however that may have taken place. On this subject we shall probably most of us still agree with the opinion of Darwin[2], that we are not in a position to even speculate or think upon that question, — that any speculation about it is almost a waste of time. And this, I think, remains true in spite of the magnificent results of the organic chemists in producing chemical bodies by synthesis, which before had been regarded

[1] Read February 7, 1894.

[2] In Life and letters.

as capable of being made only in the laboratory of the living body. Many of these can now certainly be produced, but that is very different indeed from creating protoplasm endowed with life; and so far are we from achieving this by any chemical means, that I think we may venture to dismiss all consideration of the ultimate origin of life.

But granting the origin of living matter, these theories of evolution which we are considering and hope to discuss to-night can deal with it, and with their help we believe that we can account for what has subsequently happened; namely, the evolution of all forms of life, animal and vegetable, upon the surface of the earth.

The first of these theories which I propose to discuss is the well-known Darwin-Wallace theory of natural selection, with its three factors.

First, individual variation, — the fact that individuals differ, and that the differences are essential or inherent in the organism, so that even if animals were brought up alike, we know they would still be unlike, and so that, however much the offspring may resemble their parents, they are never exactly like their parents or exactly like each other. There is, then, first, individual difference, one of the most essential facts in the organism.

Secondly, the fact of heredity,— the fact that these inherent differences may be and are inherited. Although the hereditary transmission of acquired differences is disputed, the transmission of those that are inherent is certain. This stands before us as one of the most obvious and certain of conclusions, equally proved by the observation and experience of every one of us.

Thirdly, the fact that there must be a struggle for existence; that there are far more individuals born into the world in every species, even the most slowly increasing, than can possibly survive and reproduce.

These three factors must by logical necessity lead to a survival of the fittest among individual variations. It does not require a scientific mind to comprehend that, — to infer that some amount of evolution must ensue from the co-operation of those three factors, every one of which stands firm and undisputed. Among all the advocates of rival theories which have been brought forward to explain evolution, no one has ever ventured to attempt to disprove any one of these three factors. They stand unchallenged.

The politician, Henry Fawcett, saw, long before scientific people themselves understood what Darwin meant by natural selection, that logically some result must ensue from such co-operation. Fawcett said that natural selection must produce evolution as surely as a round stone will roll further than a square one. Some measure of evolution is simply the logical result of the co-operation of these three undisputed, abundantly proved factors.

Now, some writers have thought to undermine the theory of natural selection by arguing that the important and essential factor of individual variation is not explained by the theory which rests upon it. True, it is not; but for the theory of natural selection, the explanation does not signify. So long as individual variation is present, so long as it is hereditary, it does not signify how it is produced. There are, indeed, many theories professing to account for it; but biologists are not generally agreed as to the manner in which it is produced. But so long as it is there, it is available, and natural selection can make use of it.

It is interesting to note that, when Newton discovered the principle of universal gravitation, some people maintained that he had discovered nothing because he had not explained what gravity itself was. Now after two hundred years we can safely assert that universal gravitation stands out as one of the most triumphant discoveries of the human intellect; and yet we, even now, are just as much in the dark as to what gravitation itself is as when Newton wrote. Exactly so it is with regard to individual variation. So long as it is a fact essential to organic nature, that one individual must be different from another, and so long as these differences are hereditary, so long may natural selection have abundant material for its work, even though it is unable to explain how that individual difference is produced. I am very far from undervaluing the interest of such an explanation; on the contrary, I maintain that it forms one of the most interesting of biological problems now before the scientific world, or likely to be before it for many a day.

In fact, every successful attempt at scientific explanation only interprets down to a certain level of causation; and this is just as true of universal gravitation and natural selection as it is of smaller efforts. Down to a certain level of causation, natural selection explains at any rate some part of organic evolution. A more fundamental level would be to explain the factors upon

which natural selection itself depends; but because we have not yet reached that lower level, we have no reason for doubting, as some would believe, the complete efficiency, at its own level, of the explanation we do happily possess.

The theory which stands in contrast with natural selection, and which has been here supported more fully than in any other civilized country, with the exception of France, is the theory we usually attribute to Lamarck. Erasmus Darwin in England, however, has the priority, in that he first brought forward the principles which Lamarck more effectively supported. But to Herbert Spencer belongs the chief credit, because he has taken that part of the earlier theory which is acceptable to modern biological thought, and upon this basis has formed his great theory of evolution.

Lamarck believed in an innate tendency toward perfection in animals. Now, that is a view which very few zoologists at the present time, if any, would dare to sustain. In fact, an evolution due to an innate principle of perfection is not very much removed from the doctrine of special creation which preceded any theory of evolution. Herbert Spencer, therefore, rejecting all those elements of Lamarck, which the scientific world could not possibly accept, has taken that which has commended itself to science, and upon it has formed his great theory of evolution; so that the Lamarckian theory, as presented to the world to-day, comes before it in Spencerian language and in the closest relation to Spencerian thought. In saying this, however, I do not by any means intend to be understood as supporting Spencer's theories or the views upon which he bases them.

The Lamarckian theory, then, upon which Spencer has based his philosophy, is a theory of evolution dependent, not like natural selection upon three factors, but upon two. It depends first of all upon the effect wrought on the individual by that which happens during its lifetime. Instead of depending on those innate and essential differences upon which natural selection rests, this theory depends on those changes which are caused during the life of the individual,—the action of some external force upon it, the effect of its own will, the changes produced by the use and disuse of its own parts. The Lamarckian theory depends in fact on all those changes in an individual which we now call its acquired characters; that is, characters which the individual has

come to possess but which were not potentially present at the beginning of its separate life.

The first factor, therefore, is made up by changes that are wrought in this way. The second factor is heredity, by which it is supposed that these changes are transmitted; and it is certainly true that if such transmission is possible, some amount of evolution must result. You will all be prepared to admit that if these two factors represent facts, their co-operation must produce some amount of evolution.

It is important to remember, however, that both factors are not undisputed, as are the three factors of Darwinian evolution. Although we all admit the existence of acquired characters as the effect of external causes upon the individual during its life, yet biologists are by no means agreed that these effects are hereditary, and, if not, the acquired character ends with the individual in which it arose, and, not being handed on, can never become a character of the species. It is impossible for those wh hold the Lamarckian or Spencerian view to escape from this. If it is true that such characters are transmitted, then the foundation of the theory is secure; but the transmission of acquired characters is by no means proved. Herbert Spencer has preferred to occupy himself in rearing a magnificent edifice upon this foundation, rather than employ his acute intellect in testing its firmness and security in every possible way.

So far as observation goes, all those characters which are believed by many to owe their origin to the Lamarckian principle, are present in the individual before the beginning of its active life, before the operation of those causes which were believed originally to account for the characters. According to the Lamarckian theory such characters have already become hereditary; and therefore it is of essential importance to the Lamarckian to prove that acquired modifications can be and are transmitted. Only in this way can he give good grounds for the opinion that such characters, when they occur ready-made in the individual, are to be explained by the action of external causes during the lives of ancestors.

These are the two main theories of evolution. There are several others, upon which I will dwell only for a moment because these two alone command any very large amount of attention at the present time.

In the first place, Lamarck's theory of the innate tendency towards progressive perfection in animals is not held in exactly that form, but some zoologists in this and other countries believe that they see evidence in the rise and fall of certain groups of fossil animals for the existence of a tendency towards extinction, or a tendency towards sudden growth, which lies within the animal itself and is not determined by any external cause. That is a very close approach to Lamarck's original principle of an innate tendency in one direction or another. I will not discuss it at any length, because I think that this evening if we get some idea and have some discussion on the merits of the two main theories of evolution, that will be as much as we can expect. I will only say with regard to the subject that arguments based upon fossil remains are apt to be somewhat dangerous, because we have, at least so far as the conditions of life are concerned, so small an amount of evidence. In certain parts of Africa, for instance, the presence of the tse-tse fly absolutely limits the existence of some of the larger quadrupeds. Wherever that fly is, the animal cannot exist. It is very possible that in future times skeletons will be found in specially large numbers on the borders of districts where the fly abounded, and any attempt to argue, from the appearance of the skeletons themselves, as to the causes of this great extinction will obviously be entirely false and misleading. We have in the skeleton of an animal so smal. an indication of the events of its life and the conditions of its death, that it is, except in very rare cases, most unsafe to argue as to the causes of its extinction.

Another theory of evolution is one which has been brought forward by Professor Geddes of Scotland. He believes that there is an innate tendency towards growth and towards that dissipation of matter which constitutes its reverse, — the anabolic and katabolic tendencies, as he calls them. But that view, although he argues it with much eloquence, has not been widely accepted, and I think it will be generally admitted that it does not yet rest on sufficient proof.

In addition to these, there are some who maintain the position that there is an unknown cause of evolution. They believe that these theories, although one or more of them may be of value, are yet insufficient to account for organic evolution. Those who take this line are of course logically bound to bring forward the

classes of facts with which no existing theory is, as they maintain, competent to deal.

All we shall have time for to-night is briefly to compare natural selection, the Darwinian interpretation of evolution, with the Lamarckian theory. It is interesting to note that, although they are so essentially distinct one from another, in earlier times these two theories appear to have been entirely confused. Lamarckian evolution, Spencerian evolution, appeals to the mind of man far more strongly than Darwinian evolution. Any one of us, were we to have created the organic world, would certainly have created it according to Lamarck. We should have made evolution by use and disuse of parts, and not by natural selection. However, we are not concerned with the sort of world that we should have created. The question before us as scientific men is not what might have happened, but what has happened. Nature, as I have heard Prof. Michael Foster say, has a very queer way of going by roundabout paths and refusing to take the roads we should lay out for her ourselves, and which we look upon as the most direct and obvious. The fact that the general aspect of the Lamarckian theory commends itself to the human mind affords no reason for looking upon it as the correct one, as opposed to the Darwinian theory.

The Duke of Argyle, who is still strongly antagonistic to natural selection, a few years ago wrote an article in the Nineteenth century called "The power of loose analogy." By this title he intended to imply that those who believe in natural selection have been led away by the specious character of the words themselves. I suppose that the Duke feels himself bound to account in some way or other for the fact that people believe in natural selection, while he does not, and accordingly he suggests that the seductive power of the title employed by Darwin has misled the scientific mind into a belief in the process itself,—only rare and subtle intellects like his own being proof against such an allurement. *Natural:* a word expressive of familiar objects and processes always around us. *Selection:* a process with which we are all familiar. In this way it seems reasonable to the Duke of Argyle to suppose that men have been misled by the seductive nature of the terms employed by Darwin. The terms applied to processes familiar to every one, and therefore every one accepted them at once, without inquiring what they

really meant. This is, of course, an explanation eminently satisfactory to the single writer who was not to be convinced by "the power of loose analogy." But when we proceed to test this ingenious suggestion, and look into the history of the times to which it applies, when we read Darwin's letters, we find that he continually complains that people do not understand what he means by natural selection, and he almost regrets having used these words. He says more than once that he wishes he had used Herbert Spencer's term, the survival of the fittest, because his own title, natural selection, is comprehended with such difficulty.

When we look to another class of evidence we find equally sure ground for the conviction that natural selection was driven into men's minds with the very greatest difficulty, and by no means with the ease which the Duke of Argyle assumes. It is very interesting to consult the various skits written between twenty and thirty years ago, and in which the writers supposed that they were making fun of Darwin's theory. If you will read them, you will be struck by one very remarkable fact: their authors are all making fun of Lamarck when they believe they are making fun of Darwin.

I remember once seeing a picture in Punch, representing the evolution of the power of flight by the human species. It represented a man standing upon the roof of a house and waving his hands, which, in consequence of the use to which they were put during his individual life, grew somewhat in size. Passing down to the next generation, his son was found waving rather larger hands, and the waving made them still larger. In the course of generations the descendants acquired large wings and flew down from the roof of the house. That was supposed to be a parody on evolution according to Darwin. I have called it a skit, but you will see at once that you cannot get a better illustration of Lamarckism. It *is* Lamarckism. It is not making fun of it; it is a description of the process itself.

Then Lord Neaves wrote a song in which he attempted to make great fun of Darwin's theory. It was a very long song, many verses of which were skits upon Lamarck, while supposed to be skits upon Darwin.

> "A deer with a neck that was longer by half
> Than the rest of its family's — try not to laugh —
> By stretching and stretching became a giraffe,
> Which nobody can deny."

This is pure Lamarckism. The evolution was supposed to be caused by stretching without any selection at all.

The best example of all, however, is given by Mr. Courthope, in his "Paradise of birds." I commend his account of the evolution of birds and mammals to those who believe the Lamarckian theory. He tells us there about the Ornithorhynchus, which he commends as a very prudent beast:—

"For he saw in the distance the strife for existence,
That should his grandchildren betide,
And resolved, as he could, for their ultimate good,
A remedy sure to provide;
With that, to prepare each descendant and heir
For a separate diet and clime,
He laid, as a test, four eggs in his nest,
But he only laid two at a time.
On the first he sat still, and kept using his bill,
That the head in his chicks might prevail;
E'er he hatched the next young, head downwards he slung
From the branches, to lengthen his tail.
Conceive how he watched till his chickens were hatched,
With what joy he perceived that each brood
Were unlike at the start, had their dwellings apart,
With distinct adaptations for food.
From the bill, in brief words, were developed the birds,
Unless the tame pigeons and ducks lie;
From the tail and hind legs in the second-laid eggs,
The apes and—Prof. Huxley."

If we now turn to the skits on evolution written at the present day we find they are very different. Miss May Kendall, in writing her "Ballad of the Ichthyosaurus," only a few years ago, says:—

"E'er man was developed, our brother,
We swam and we ducked and we dived,
And we dined as a rule on each other;
What matter? The toughest survived."

This is true natural selection. The authoress understood what she was talking about. And even long ago, at the time when those mistaken parodies were written, intended for Darwin and really applying to Lamarck, we find an acute mind like that of James Russell Lowell, in the Biglow papers, making fun of Darwinian evolution:—

"Some flossifers think thet a fakkilty's granted
The minnit it's proved to be thoroughly wanted,
Thet a change o' demand makes a change o' condition,
An' thet everythin' 's nothin' except by position;
Ez, fer instance, thet rubber-trees fust begun bearin'
Wen p'litikle conshunces come into wearin',
Thet the fears of a monkey, whose holt chanced to fail,
Drawed the vertibry out to a prehensile tail."

That is a most ingenious and interesting parody, making the theory of natural selection apply to the individual instead of to the species. The writer pretends to suppose that a quality is gained in the course of the individual life, because of the individual need; whereas under natural selection it is gained in the course of many generations by a need which is imperative enough to cause the extinction of individuals without the quality, or with it in a comparatively slight degree.

Another interesting question has been raised by Mr. Lloyd Morgan, as to whether the phrase "natural elimination" would not be a more correct one than "natural selection." The process is, of course, selection by and through elimination. The survival of the fittest means the elimination of the unfittest.

The relation between selection and elimination has been put in a very striking way by Mr. Samuel Butler, who says that according to natural selection we are what we are, not by the successes of our fathers and mothers, but by the failures of our uncles and aunts. The question is, shall we dignify with the title of this important cause of evolution those who have failed in the struggle, and do not happen to be the ancestors of any living species, or those who have succeeded in the struggle and are now abundantly represented by descendants? I think that "natural selection" forms on the whole the best term for the process. It has the advantage, also, of being the historic term proposed by Darwin.

Another important point in favor of "natural selection" as a term, is that it suggests a parallelism or comparison with the process of artificial selection. Yet another point is the fact that you may find in the words themselves all the three factors obviously suggested; for selection would be impossible without individual difference, and it would be useless unless these differences were hereditary; and, furthermore, selection implies something which selects; that is to say, the conditions of nature,

the rate of increase with its result, the struggle for existence. So that the three factors of natural selection are implied by the very words themselves.

Now I want very briefly to bring forward the chief objections that have been urged against natural selection. In the first place, if natural selection be true, all the varied characters of animals and plants must prove to be useful to the possessor in the struggle, or to have been useful at some time in its history.

We are only required, however, to prove utility as regards undoubted characters of the species, and these are hereditary, and we must put on one side certain characters which are confined to the individual in which they appear. For instance, if it were proved that the Mollusca of any one river differed from those of the same species in another river, but that the differences were confined to the individuals in which they occurred, so that if these Mollusca were placed when young in the second river, they would come to resemble those which were proper to it, then we should not be concerned with characters of the species at all. The language spoken by a nation similarly is not a character of the human species, for we know that a child of another nation would acquire it perfectly together with the particular modes of thought and expression tortuous or direct which are associated with it. These results of environment are not characters of the human species. The individuals of the human species come into the world with a certain elasticity, a certain power of being developed in various directions. But although the elasticity itself is a character of the species, and is inherent, the particular quality in which it may result when operated upon is certainly not a specific character.

The more we work on the characters of animals in general, even though we at first can see no utility, the more we come to admit this principle, and to believe that either now or in some past time, the characters have been useful. I can certainly say of many characters which I have studied in some of my investigations, that at first they seemed to be meaningless, but afterwards appeared to be of much importance in the struggle for existence. I think we may safely assume with regard to many characters of which we can now see no explanation that by and by the explanation will be forthcoming.

Being unable to prove utility does not invalidate natural selection. If inutility could be proved for any large class of characters, the theory would certainly be destroyed as a wide-reaching and significant process. I do not think, however, that any such evidence has been forthcoming. I shall be interested in the discussion which follows this paper to hear whether those who believe in the Lamarckian theory have any such evidence to produce, whether they can prove that any one great class of characters has been useless in the past and remains useless in the present.

Another class of objection has been urged long ago, and is still urged to-day. Why do we not find in the paleontological series the records of failures? Now, as regards the individuals of a species we cannot expect to find any such evidence. What is failure? Failure means, according to natural selection, the failure to produce offspring. The individual which comes into the world and dies young has failed. The individual which is represented in the generations of the future has succeeded. Natural selection has set its stamp upon that individual. But it is impossible to say whether or not this is true of any particular fossil. We have not got the facts before us by which we can form any conclusions.

Furthermore, we know the struggle for existence is excessively complicated. The skeleton *alone*, though of the highest value in association with the rest of the organism, has been the turning point in the struggle in a comparatively small number of cases. When it has been the turning point in association with other parts, these latter are absent. We have only a very small part of the problem before us, and never can expect any more.

But while we cannot expect to find evidence of the survival of the fittest among the individuals of a species, we may expect to find it in the supplanting of classes by classes, of groups of species by groups of species. Some of the facts which have been brought forward as evidence in this direction do, to my mind, very strongly support the theory of natural selection by paleontological evidence. Consider especially the case of the large mammals preceding those which gave rise to the quadrupeds now upon the earth. So far as we can judge of these huge forms by their skeletons, they appear to have possessed a bodily structure as well fitted to survive as that of many now living in the world;

but they differed from these latter in that they had extremely small brains. We can easily understand that inferiority of intellect would cause them to be worsted by animals which were in other respects no better endowed.

Exactly parallel is the relation of man and the apes. In bodily structure the difference is insignificant. In the brain, however, we meet an important and essential distinction. It would appear here that natural selection has taken one particular part of the organism of paramount importance in the struggle, and has developed that rather than made a change along the whole line.

We see the same relationship in the gigantic reptiles of the secondary period as compared with the mammals of the Tertiary. The latter with their larger brains and higher intelligence were able to supplant the former, just as they have in turn been supplanted by the still larger brained animals whose descendants now people the earth. All this seems to me to afford very strong support to the theory of natural selection.

Passing now to another class of objections: natural selection, it is said, can never account for the beginnings of things. Until an organ is raised to a useful level, selection can have nothing to do with it. At first sight that is a serious objection, but it suggests its own answer; viz., that an organ so rarely develops *ab initio*. Organs are not formed anew in an animal, but they are formed by the modification of pre-existing organs; so that, instead of having one beginning for each organ, we have to push the beginning further and further back, and find that a single origin accounts for several successive organs, or at any rate several functions instead of one.

The typical vertebrate has four limbs. These in fishes are used for swimming, while in terrestrial forms the same limbs are modified and used for walking. New organs are not introduced, but the old are modified for a new purpose. When the terrestrial form again becomes aquatic, the limb that was used for terrestrial progression is modified back into a functional fin; and again, when flight becomes necessary, the same organ is used for the new function. So that whatever the changes in the mode of progression, we need no new organ at all; for the old organ is used for the new purpose. It is very much easier to understand how a useful level can be attained in that way than by organs starting *ab initio*. But of course we must come down to a true

beginning if we push our inquiries far enough. In attempting this, we are carried to those remote times in which the ancestors of vertebrates arose. Upon these forms we can do no more than speculate, but it is at any rate impossible to prove that four bud-like projections from the body may not have been useful, from their very beginning, to a slender worm-like animal in pushing its way through mud or thick weeds. Dr. E. B. Tylor has told me that he believes that the same thing holds with regard to human weapons. He said that, in examining ancient weapons, he was often struck with the fact that a weapon or implement had ultimately turned out to be so very much more useful for a new purpose rather than that for which it was originally formed. Here, then, one origin apparently accounts for several forms of implement.

Another objection raised against natural selection is that a selective cause is never a true cause. Professor Cope means to imply that when he speaks of the "*Origin* of the fittest." But Darwin's argument on this point is perfectly sufficient. He says that when a man drops iron into sulphuric acid, he does not originate the chemical force that operates, but he may be fairly said to make sulphate of iron. So natural selection does not itself originate the factors upon which it depends, but it is so essential to the result that it may be fairly looked upon as the true cause (at that level of causation). In Galton's work we have a most complete inquiry into human variation and its inheritance, and he shows us that such variation by itself, unguided by selection, can never advance to anything. Even if you start with ancestors who are remarkable for any intellectual or structural feature, their descendants, although some of them may partake of their parents' peculiarities, sometimes even to an increased extent, will ultimately return to the pattern of the race. There is always a "recession towards mediocrity." Hence, unguided variation can never explain the "origin of the fittest." Such a view is entirely contradicted by the results of Galton's researches. Any marked change in the direction of fitness can only become a character of the species by accumulation through many generations, and this can only take place by natural selection. Variation unguided by selection can never advance on the increase of fitness present among the individuals of a single generation; and even these improvements, if relatively marked, can never become

a character of the species without selection, but by recession will tend to be lost in the subsequent generations.

I have briefly touched on some of the chief difficulties which are advanced against natural selection. I now propose to devote the remaining part of my time to the difficulties which seem to me to apply to the Lamarckian theory.

Lamarckian evolution, as I have mentioned before, depends upon acquired characters. A good deal of misconception has arisen from this use of the word "acquired." An acquired character has sometimes been interpreted to mean any character that an animal has come to possess; hence, inherent and acquired characters have been confused. The word "acquired," as used by biologists, must be understood to have a limited and special application, meaning only those characters which have been produced in the organism by the incidence of external forces, or by the action of its own forces, use and disuse of parts, and so on, during its life. Weismann has suggested the term "blastogenic" for characters potentially present in the germ at the very beginning of life, and "somatogenic" for those which appear afterwards and are not potentially present in the germ. Here blastogenic is the equivalent of inherent, and somatogenic of acquired.

Some years ago I suggested that the terms "centripetal" and "centrifugal" might be employed to express this acquired difference, acquired characters being centripetal, because they are impressed upon the body or one of its parts from without; inherent characters being centrifugal, because, arising from within, due to the essential nature of the organism itself, in the course of development they come to appear, as it were, on the surface as visible features.

When we now consider the transmission of acquired characters, upon which the Lamarckian theory certainly depends, we are led first of all to inquire whether it is possible to frame a theory of heredity within which such transmission can be included. If, for instance, there is a change in the brain of an animal, owing to the exercise of some part of it, how can such a change in the brain-cell be transferred to the germ-cells of the animal, so as to be transmitted to its offspring? It may be objected, if you can prove that such transmission does take place it is no matter how it takes place. Quite true, if the evidence is sufficient and indisputable. But we must remember that the amount of evi-

dence required in order that there may be sufficient, depends upon the probability or improbability of the thing to be proved. This view is extremely well put by Professor Huxley in his memoir of Hume, where he says that if any one came to him and stated that he had seen a piebald horse in Piccadilly he would be prepared to believe it; that he might require confirmatory evidence if the statement were that a zebra had been seen; but that if even the friend in whom he trusted told him he had seen a centaur trotting down that eminent thoroughfare, he should emphatically disbelieve it, and that nothing short of a monograph on the anatomy of the centaur by a comparative anatomist of the stamp of Johannes Müller would convince him that the observation was correct. We are compelled to admit that the amount of evidence we require does to a great extent depend upon the inherent probability or improbability of the conclusion to be sustained. If it appears to us to be almost impossible to conceive of a mechanism whereby an acquired character can be transmitted from the outlying parts of the organism to its germ-cells, then we have every reason for scrutinizing most carefully any evidence that is alleged to prove such transmission.

Let me first of all give you a concrete example which is frequently brought forward by those who believe in the Lamarckian theory in this country, and have chiefly studied the skeletons of Mammalia. They say the joint of an animal possesses just the sort of shape that would be produced by the motion of the joint itself, and they urge that the joint as we see it has arisen from the hereditary effects of that motion. They look upon this as a very satisfactory explanation, because they consider it to be so obvious and fundamental. You do not require anything further, selection is unnecessary and even the individual variation—so mysterious a factor of the Darwinian theory—is here entirely explained.

But is the interpretation valid? In the first place, it is clear that such an hypothesis can never afford a wide or general explanation. There are a great many parts of the animal body which are not modified in their use. You cannot thus explain the growth of hair, or the color upon the surface of the organism. For these and other useful but passive structures, the Lamarckian interpretation will not hold at all. Hence we may divide the organism into two sections, to one of which the Lamarckian

theory might be held to apply, and to the other the Darwinian alone.

But upholders of the Darwinian theory consider that it applies to the other section as well. They point out, that while the form of the joint is the sort of form that would be produced by the motion, such a form is the only one which admits of convenient motion, that motion has been essential to the life of the organism, that alert and rapid movements have been a necessity in the struggle for existence, and that any form which would prevent or clog the movements would be at once destroyed by the operation of natural selection. Natural selection they hold to be competent to explain these parts which the Lamarckians also claim to explain, while it offers the only explanation of the other parts.

If we suppose that Lamarckian evolution in part explains the actively used organs, and Darwinian evolution in part, we should expect that modification would take place more quickly in that section of the organism where the two principles were at work than in the other section where only one principle—the Darwinian—can play a part. But there is no evidence of such especially rapid evolution. It seems to me that we are in a position to use the old principle of cutting off superfluous causes. No unnecessary cause should ever be introduced into an explanation, and if Lamarckism, untenable in the one section, is superfluous in the other, it should be removed, unless there is very clear evidence proving that it has been at work.

Furthermore, in certain cases, such as the protective attitudes and appearances assumed by many animals, we meet with clear evidence that the two kinds of parts—those that are effected by their use and those that are not affected—have undergone development together, suggesting strongly that their evolution has been under the direction of one set of forces, and not of two sets which have little in common.

Having now brought forward certain general objections to the Lamarckian position, let me take exception to one or two special cases.

Certain animals, such as lobsters and crabs, have the power of very readily parting with some of the most important of their members. The large claws are easily thrown off, and this may be of great advantage in the struggle of life, because when an

individual is attacked by an enemy and seized by the claw, it has a chance of escaping. In the case of the lobster, the dismembered claw may not let go of the enemy although the enemy may let go of the claw. The claw may take charge of the enemy while the lobster escapes.

Now that is a very interesting adaptation. We find the claw so formed that it can be thrown off, but even when thrown off it continues to be of much use to the organism. Its nervous and muscular mechanism is so arranged that mutilation actually stimulates it to contract, and it continues to hold the enemy. In the case of certain crabs, the dismembered claws keep snapping and jumping about. The same is true of the tails of many lizards, which, when thrown off, will jump about in the most active way, distracting the attention of the enemy, while the lizard makes its escape. Here, too, mutilation stimulates the nervous and muscular mechanism in tail and claw.

In these cases of actively used parts of the organism the Lamarckian interpretation is absolutely at fault. You cannot apply it. It is impossible to explain upon the theory of the transmitted effects of use and disuse. No activity manifested by the tail after it has ceased to be part of the lizard can ever be transmitted. Not only that, but all development undergone by the tail from the effects of use and disuse, etc., up to the time of its severance, is also lost to the individual, and cannot be hereditary. And so with the claw. The large claw is the most important appendage of the lobster, and yet it is probable that most lobsters lose it many times and grow a new one. We have here a very specialized organ with very remarkable functions continuing in ever an increased degree after severance from the animal; all this is readily explained by the Darwinian theory, but cannot be explained by the Lamarckian.

The same inadequacy of the Lamarckian theory is forced upon us when we look a little more deeply into the nature of the process which is supposed to occur. The Lamarckians attempt to explain joints and some other structures by the effects of stress and pressure, but when we look into the matter a little, we find that the explanation is not so complete as it is supposed to be.

For instance, it has been believed in this country by many distinguished biologists that the complex shape of mammalian teeth is due to pressure produced by mastication. As the pressure

has been applied to the tooth, so has the tooth grown. But would pressure produce such an effect upon a tooth? That is certainly not our experience. Pressure and friction have an unfortunate way of wearing a hole in the tooth, rather than causing it to grow an elevation. As a matter of fact we know that the shape of teeth is predetermined long before they are cut in the soft dental matrix beneath the gum. It is not a question of the transmission of acquired characters, but the supposed transmission of a character which the parent cannot by any means acquire. Teeth, so far as they react to pressure or friction can only react by wearing away. With regard to the joint, we are told by some Lamarckian writers, that pressure and friction produce the reverse effect and wear away cavities rather than cause new growth.

I was reading a most interesting paper by Dr. Wortman of New York, the other day, attempting to explain the occurrence of a furrow in a joint, owing to the pressure of a corresponding ridge. The pressure of the ridge, it was said, produces a furrow in the opposite side of the joint. It seems to me that in this we are going a little beyond what physiology and histology teach us. It seems to me to be a blind appeal to mechanical forces unsupported by any adequate investigation of the physiology and histology of the tissues concerned. Is it likely that a bone would react to intermittent pressure by producing a furrow? It is far more probable that the reverse effect would tend to be produced.

I will only ask one more question with regard to this matter of use and disuse, and that is, why, if you are going to explain any of these parts by pressure and friction, should the process be stopped when a useful level is reached? If the pressure does cause such effects and they are hereditary, how are they prevented from increasing beyond all bound in the course of generations? Why should pressure on teeth cease to produce further growth, when the tubercle has reached its proper height? It seems to me that the fact that all these shapes of bones and teeth just reach and stay at an adaptive level is the strongest evidence that they are not produced by the operation of mechanical forces, but by natural selection.

We now pass to the consideration of indirect evidence: that it would be impossible to explain evolution without the Lamarckian theory.

Time will permit me to deal with only one class of characters, and that is associated with the nervous system and manifested as instinct. These instinctive actions are generally thought to be the strongest evidence in favor of Lamarckian evolution. It has been argued that we cannot explain the instinctive action of animals — the wonderful instincts which are due, as we know, to modifications of the nervous system, — except by supposing that animals have intelligently modified their actions in consequence of experience and observation, and that the result has then been transmitted and has become the non-intelligent instinct of their offspring. If we had no other explanation of instinctive action, such an interpretation would constitute a strong support to the Lamarckian theory.

I do not, however, believe that this is the only, or, indeed, the correct explanation of instinct. In considering this question, we must distinguish between the instinct manifested by many of the higher invertebrate animals and much that we are apt to call the instinct of the vertebrates. A great many actions which are put down to instinct in the higher vertebrates, such as birds and mammals, are not instinctive at all, but merely the result of observation during the life of the individual. We see an example of this in the action of the seal which, as Nansen tells us, took up a position on the outer ice-floes to escape the dangers of the polar bear, and afterwards incurred this very danger on the inner floes to avoid the greater peril from the hunter. This is a clear case of reasoning from the results of observation, and no instinctive avoidance of danger. So also with a bird which flies away if you have a gun in your hand, but allows you to come near when you have a walking-stick. This is the result of reason and not merely instinct; and we must carefully distinguish between a lesson learned by the individual, however well learned and easily repeated it may be, and a true instinctive action which was never learned at all but sprang fully formed into existence. Such true instincts certainly occur in the higher vertebrates, such as the act of sucking performed so perfectly without any education or practice by the newly born mammal. In the lower animals such true instincts are relatively far more numerous and play a most prominent part in the life of the individual. In these cases of true instinct I would suggest that we are dealing with actions which have never been intelligent at any time in the past history

of the species, and which have been due to the operation of natural selection upon the nervous system. Certain cases which are most strongly held to be the outcome of the transmission of gained experience and the acquired results of practice certainly cannot be explained in this way.

For instance, how upon any such hypothesis can you explain the wonderful structure of the cocoon spun by the larva of an insect? The view would be, I suppose, that the ancestral larva spun a cocoon which was not much of a success and was in consequence attacked by enemies; that the larva observed these attacks, and accordingly improved its cocoon. But that is not the way in which the struggle for existence is waged with insects. If the larva failed, it failed, and that would be the end of the matter. It has no chance of improvement; it has no opportunity of learning by experience. Its only chance of survival is to avoid experience of foes altogether; experience is the most dangerous thing in the world to an edible insect. This becomes still more obvious when we remember that failure or success is almost always determined long after the cocoon is made. The caterpillar perhaps spins the cocoon in autumn, but the real stress of competition will come in winter, when insect-eating animals are pressed hard with hunger and search high and low for food. But the caterpillar by this time is a chrysalis and of course has no opportunity of improving the cocoon. The selective test is applied long after the operation has been performed, and when there is no possibility of gaining by experience. We are thrown back, then, solely upon natural selection, which acts on the nervous system of the caterpillar, and thus compels it to make the cocoon in a certain way. In other words, those caterpillars which are impelled by their nervous system to make ill-formed, conspicuous cocoons have no chance of living, and in future stages producing offspring. Hence, the selection caused by the keen sight of foes first raises and then maintains at a high level the standard of cocoon-making.

This contention as to the uselessness and danger of experience applies to the whole of those smaller defenceless animals which have no chance of fighting with their enemies or of escaping when once they have been detected.

Another special kind of instinct has been greatly relied on by Romanes as evidence for the Lamarckian theory of transmitted

experience. Certain Hymenoptera allied to wasps possess an instinct which leads them to sting larvae and store them up in their nests as food for their young. It is generally believed that the larva is stung in the central part of the nervous system so that it can no longer struggle. I say "generally believed" because it has been pointed out to me by so distinguished an observer as Dr. Peckham of Milwaukee, that certain facts are opposed to the generally received account. It is to be hoped that the observations which are chiefly due to Fabre will be repeated and tested as minutely as possible. The prey is stored up in the mud-tube or burrow of the hymenopteron, and keeps perfectly fresh because it is alive, although completely paralyzed. Larvae stored up in this way appear to live much longer than those which, in the full possession of their faculties, are deprived of food.

Now this is a very wonderful instinct, and it has been argued that here is a case which cannot be explained except on Lamarckian lines. I maintain, on the contrary, that it is a case which cannot by any possibility be explained on Lamarckian lines.

The wasp-like insect has no opportunity of learning by experience because it can never know whether the larva stored up is a failure or a success. If the larva had not been stung, or, accepting the received accounts, had been stung in the wrong place, it would struggle and perhaps kill the young grub; or dying of starvation it might dry up and be useless as food. But the hymenopteron never goes back to inquire. It makes all the difference to the young grubs whether the food provided for them is in an appropriate condition or not, but it makes no difference whatever to the parent insect. The latter seals up the chamber in which its eggs have been laid and never opens it again; it has no chance of noting the failure or success of the food it has provided. It is clearly a case like that of the cocoon which cannot be explained on the Lamarckian theory and must be explained on the Darwinian. And this latter interpretation is easy: those insects which possessed the nervous mechanism impelling them to provide food in an appropriate condition gave to their offspring the opportunity of surviving and inheriting the same instinct. While others, impelled to perform less efficient actions, were thereby cut off from any representation in the next generation.

If the origin of wonderful and complex examples of instinct such as these cannot be explained by the Lamarckian theory but readily by the Darwinian, why should not natural selection also offer an adequate explanation of all other cases?

I have already taken up a great deal too much of your time. I much hope to have the opportunity to-night of hearing many stronger arguments in favor of the Lamarckian theory than it has been my opportunity to hear hitherto.

Note.—In revising the short-hand transcript for publication, I have not made any changes which alter the character of the address. It remains the record of a spoken address, the sequence and continuity of which were maintained by the use of brief notes. I have not verified the quoted opinions and words of others, and there are probably verbal errors. I believe, however, that in every case the true meaning of the author has been preserved. —E. B. Poulton. Oxford, May 21, 1894.

A REMARKABLE ANTICIPATION OF MODERN VIEWS ON EVOLUTION.

THE great pioneer of modern anthropological and ethnological research—James Cowles Prichard, was born at Ross, in Herefordshire, 11th February, 1786. The following brief account of his life is taken from Professor E. B. Tylor's article in the *Encyclopædia Britannica* (1885, vol. xix., pp. 722, 723). Prichard was brought up as a member of the Society of Friends, to which body his parents belonged. He joined the medical profession, taking his Doctor's degree at Edinburgh, "afterwards reading for a year at Trinity College, Cambridge, whence, joining the Church of England, he migrated to St. John's College, Oxford, afterwards entering as a gentleman commoner at Trinity College, Oxford, but seeking no degree in either University. In 1810 he settled at Bristol as a physician." Among his many great achievements in anthropology was the proof "that the Celtic nations are allied by language with the Slavonian, German, and Pelasgian (Greek and Latin), thus forming a fourth European branch of the Asiatic stock (which would now be called Indo-European or Aryan)". His treatise on the subject, entitled "*Eastern Origin of the Celtic Nations*," appeared in 1831. "It is remarkable that the essay by Adolphe Pictet, *De l'Affinité des Langues Celtiques avec le Sanscrit*, which was crowned by the French Academy and made its author's reputation, should have been published in 1837 in evident ignorance of the earlier and in some respects stricter investigations of Prichard."

Although Prichard's memory is much honoured, it appears that in one important respect he has not hitherto received his due. My friend Professor Meldola lately drew my attention to a section of the second volume of *Researches into the Physical History of Mankind* (2nd edition, 1826) which, as he pointed out, anticipated in the clearest manner the arguments which have been recently advanced

by Professor Weismann in favour of the non-transmission of acquired characters. The deep significance of the passages in question had been observed by Dr. Maurice Davis, J.P., who brought them under the notice of his son-in-law, Professor Meldola.

In response to Professor Meldola's invitation to prepare an account of this most interesting contribution to the history of evolution, I read the work carefully and soon found that other important ideas are anticipated in it.

Thus, Prichard apprehended with perfect clearness that domesticated races of animals and plants have been produced by the selection of man and not by favourable surroundings, careful training or cultivation. He believed in the possibility of organic evolution and supported it by excellent arguments which still have the strongest weight to-day. He even recognised the operation of natural selection although he assigned to it a subordinate *rôle*. The most important anticipation is, however, the masterly discussion on the transmission of acquired characters, a discussion in which the distinction between acquired and inherent or congenital characters is clearly drawn, and many of the most difficult cases are fully argued out, the conclusions reached being those independently arrived at by Professor Weismann over half a century later.

It is very remarkable that all this should have passed, as I believe, unnoticed. The neglect can only be explained by supposing that this particular edition was never consulted, but that Darwin and others always went to later editions of the same work. I shall be able to show that Prichard was not very confident in the strength of his own conclusions and, so far as I have consulted his later editions and works, I find reason for the belief that his convictions weakened still further. Indeed strong indications of uncertainty are to be found in the second edition itself, although they are confined to the later sections, and do not appear in close proximity to the important conclusions which they nevertheless affect.

It is certain that if Darwin had read this second edition he would have given Prichard a high place in the account

of the history of evolution which appears in the introduction to all later editions of the *Origin*. So too would my friend, Professor Osborn, have given high honour to Prichard in his interesting work, *From the Greeks to Darwin*. It is an anomaly that such works as the *Vestiges* should attract attention, while Prichard's keen insight, sound judgment, and balanced reasoning on many aspects of organic evolution should remain unknown.

I am very far from maintaining that these most interesting anticipations in any way diminish the credit of those recent writers who have treated the same subjects in greater detail and of course independently. The interest evoked by Dr. Davis' discovery in the literature of evolution is mainly due to the work of those recent authors by whom the whole subject has been brought into the light of day, and the attention of every intellectual man and woman has been compelled.

The limits of space oblige me immediately to proceed, after this too brief introduction, with a detailed statement of Prichard's arguments and conclusions, which will be found to justify, in the fullest manner, all that I have said in his praise.

It has already been said that the arguments referred to are found in the *Researches into the Physical History of Mankind*, vol. ii. (London, 2nd edition, 1826). They are included in the seven sections of the first chapter of Book ix (p. 525), which is entitled a "General Survey of the Causes which have Produced Varieties in the Human Species, with Remarks on the Origin of Nations and on the Diversity of Languages". The first chapter treats "Of the Causes which have Given Rise to Varieties in the Human Species". In the first section of the first chapter the author admits that it is fruitless to seek for a complete explanation of the causes which have produced the varieties which are witnessed in the human species. "The origin of the varieties in the breed is enveloped in the same obscurity which still hangs over every question relating to the theory of propagation."

The opinion that the different shades of colour met

with in various races are caused by climatic changes and by varying intensity in the rays of the sun, is then considered, and a great many ancient and modern exponents of this view are quoted. After reproducing a long passage from Buffon, the hypotheses of the Rev. Dr. S. S. Smith of New Jersey are described. These deal not only with the "gradation in the complexion nearly in proportion to the latitude, . . . " but also with the influence which heat exerts upon the secretion of bile. In consequence of heat "the bile . . . is augmented. . . . This liquor tinges the complexion. . . . " "Bile, exposed to the sun and air, is known to change its colour to black—black is, therefore, the tropical hue." This latter and the very similar views of Blumenbach are, however, dismissed by Prichard as "without foundation"; while as to the former suggestion of Dr. Smith, together with that of Buffon and the older writers, he observes that the principal observations on which it is based are correct. "It is certain that the majority of black races of men are inhabitants of the intertropical regions, and that most of the light-coloured nations are to be found in cold or temperate climates." But although he admits the fact, he maintains that it is capable of "a different interpretation from that which modern writers have in general adopted". He similarly admits that the skin of a European is darkened by the sun, and continues: "It seems, at first, not very improbable that individuals darkened by exposure to heat in southern climates, may have an offspring of deeper colour in consequence, and if this effect increases in every generation it may be thought sufficient, in a long course of ages, to produce a black colour of the deepest tint". But this view does not by any means commend itself to him; for he continues "that this notion, however, is altogether incorrect, I venture to conclude from the following considerations:—

"1. The progeny of individuals, embrowned by exposure to the sun, is born with the original complexion, and not with the acquired hue of the parents." Furthermore, he points out that white and black races moved respectively to tropical and temperate climates have retained their original colour for ages. The second consideration which leads him

to reject the above-mentioned conclusion is very significant, and I give it in his own words (p. 532) :—

"2. The supposition is contrary to a general law of the animal economy, according to which, acquired varieties are not transmitted from parents to their offspring, but terminate in the generation in which they have taken their rise."

The succeeding two sections are allotted to the considerations contained in paragraphs 1 and 2.

Section ii. (p. 532) is headed "Instances Showing the Permanency of Complexion in Different Races". The cases in which races have completely changed in colour after removal to a different climate he explains by a mixture of breed; and points out that "it is easy to find examples of an opposite tendency, and to show that the original hue has been preserved . . . ." Thus he brings forward the instances of the descendants of English colonists in the West Indies and Spanish in South America who "remain as fair as their European ancestors," when there has been no intermarriage with other races. "That this assertion is correct, I am convinced," he says, "by the results of repeated inquiries." In the East the same results are found, although the migration of white races into hot climates took place at far earlier dates. Thus amongst other examples he mentions that of the "white or Jerusalem Jews" who are believed to have migrated to the Malabar coast in the year 490 A.D., and whose living descendants are "said to resemble the European Jews in features and in complexion".

The converse "experiment of transplanting black races into northern climates" has not been carried on for so long a period, but Dr. Prichard points out that "several generations have produced little or no alteration in the complexion of Negroes in the United States and in other temperate climates". It is indeed stated that "the domestic Negroes who are protected from the heat of the sun by more clothing, and who pass their time in sheltered houses, are of a darker complexion than the slaves who labour half naked in the fields".

Section iii. This most significant and remarkable part

of the work is headed (p. 536), "Laws of the Animal Economy in Regard to the Hereditary Transmission of Peculiarities of Structure"; the brief title at the head of the pages runs "Laws of Nature in Hereditary Transmission". This discussion, which forestalls by more than half a century the considerations and conclusions of recent writers and especially of Professor Weismann, is opened by the statement that physiological writers have often inquired "what peculiarities of structure are liable to be transmitted by parents to their offspring, and what terminate with the individual without affecting the race. Perhaps the following remark," the author goes on to say, "may afford the solution of this inquiry".

I must now quote without any omission the succeeding two paragraphs in which the two classes of characters—inherent and acquired—are defined, as fully and clearly as they have ever been, and the opinion is strongly expressed that the former are transmissible, the latter non-transmissible by heredity:—

"It appears to be a general fact, that all connate varieties of structure, or peculiarities which are congenital, or which form a part of the natural constitution impressed on an individual from his birth, or rather from the commencement of his organization, whether they happen to descend to him from a long inheritance, or to spring up for the first time in his own person—for this is perhaps altogether indifferent—are apt to re-appear in his offspring. It may be said, in other words, that the organization of the offspring is always modelled according to the type of the original structure of the parent."

"On the other hand, changes produced by external causes in the appearance or constitution of the individual are temporary, and, in general, acquired characters are transient; they terminate with the individual, and have no influence on the progeny."

At this point the author adds a most interesting footnote in which he tells us (p. 537) that "this distinction, which has not been pointed out by any former writer on physiological subjects, was first suggested to me in conversa-

tion many years ago by Mr. Benjamin Grainger, of Derby". It would be of high interest to ascertain something more about Mr. Grainger and to find out whether he ever published on his own account. It is however probable, from the other pregnant ideas contained in Dr. Prichard's work, that the clear expression, apt illustration, and admirable discussion of these principles are entirely original.

He then proceeds to illustrate the first proposition "that all original or connate peculiarities of body are hereditary"; first instancing the well-known "porcupine family, in which a remarkable peculiarity of the [human] skin was transmitted through three successive generations," and the facts which prove the hereditary nature of complexion, as shown in section ii. Supernumerary and abnormally thickened digits are then brought forward and proved by many examples to be markedly hereditary; as also "a singular thickness of the upper lip, in the Imperial house of Austria," introduced it is believed "many centuries ago . . . by an intermarriage with the ancient house of Jagellon".

The last examples of such connate characters are especially significant. "The same observation equally applies to those minute varieties of organization, which give rise to peculiarities of habit or temperament, and predispose to a variety of morbid affections, as deafness, scrofulous complaints, and the whole catalogue of disorders in the nervous system. Even those singular peculiarities termed idiosyncrasies are often hereditary, as in the instance of a remarkable susceptibility of the action of particular medicines, such as mercury."

With regard to the second proposition "that acquired peculiarities, or characters impressed by adventitious circumstances, and not arising in the spontaneous development of the bodily structure, are never transmitted . . . " he remarks, as it has often been insisted upon since, that the conclusion "is more difficult to establish than the foregoing . . ., since the proofs must needs be of a negative kind. But," he continues, "there is no want of evidence of this description." And he again insists, as if he could not put it

too clearly and emphatically: "It seems to be the law of the animal economy, that the organization of the offspring, which as we have seen follows the type given by the natural and original structure of the parent, is unaffected by any change the latter may have undergone, and uninfluenced by any new state it may have acquired".

He then discusses the examples which are supposed to support the opposite conclusion, first mentioning the statement "that dogs and cats, the tails of which had been cut off, sometimes produce young ones which have a natural defect of the same part. It is taken for granted that these appearances are connected together in the relation of cause and effect, and therefore afford a proof that acquired peculiarities are hereditary." The author argues that cases of this kind are accidental, and he points out that such defect of parts is apt to occur in every species;—in man as well as in animals. He points to the vast experiment due to "our caprice" in mutilating the ears and tails of domestic animals, and to the effects of surgical operations upon man. What remarkable results would be witnessed if such changes were hereditary!

Professor Weismann was first led to the same conclusion as Dr. Prichard by constructing a theory of heredity which seemed to him to explain the facts and observations better than any which had been previously proposed. But the theory did not include any mechanism by which the transmission of acquired characters could take place. Professor Weismann, believing that his theory was in the main right, began to inquire for the evidence on which the belief in such transmission is based, and as soon as he commenced his inquiries the evidence broke down in every direction.

With Prichard it was otherwise, for the existing theories seem to have been against him. Thus he argues that his opponents "seem to have derived their opinion rather from some conjectural theory of generation, than from any facts which have appeared well established"; and he goes on to contend that we know so little "that we are not authorized to reason from any hypothesis on this subject".

He next deals with the statement "that after mutilation or other artificial change has been repeated through many

generations, a sort of habit may be acquired, by which the new state becomes as it were natural, and may thus modify the race". To this he replies that the evidence of such habit could only be obtained by diminishing the mutilation in progressive generations and comparing the result; whereas in all such cases the violence committed and the resulting injuries are continued unabated. "If, however, an experiment be wanting to prove that repetition effects no difference in the results," he points to the practice of circumcision which has gone on for some thousands of years without producing any hereditary change.

Prichard argues that such non-tranmission is beneficial, in fact he contends "that all the laws of nature, or the general plans which we trace through the organized world, tend uniformly to produce beneficial effects, though *particular* evils are sometimes *contingent* upon their operation". With regard to this instance he points out that, if such transmission took place, both man and animals would practically become more and more "mutilated and defective".

The author next proceeds to consider the effects of disease, introducing the subject in the following paragraph: "we cannot discern any essential circumstance in which changes produced by art or by casual injury differ from those which are effected by other external causes. We should therefore suppose from analogy that the latter are not more communicable to posterity than the former, and this presumption is confirmed when we inquire into facts."

He points out that the constitutional effects of many diseases ("small-pox, measles, scarlatina, whooping-cough"), rendering those who have suffered from them more or less immune, are never hereditary. Without attempting to explain in what the change consists, he rightly claims it as "a permanent state of the constitution, which lasts as long as the individual. . . . Those imperceptible modifications in the bodily structure which render the constitution incapable of being acted upon by certain morbid poisons are governed by the same law, as far as regards hereditary descent, as the observable changes of form which are induced by art or accident."

At this point the writer intercalates another clear statement of the essential distinction between inherent hereditary and acquired non-hereditary characters. The statement is so admirable that I quote it in full.

"We may remark in general that each individual being, through the animal and vegetable worlds, has certain laws of organization impressed upon its original germ; according to which the future development of its structure is destined to take place. These inbred or spontaneous tendencies, governing the future evolution of the bodily fabric, cause it to assume certain qualities of form and texture at different periods of growth. From these predispositions are derived the characteristic differences, and the peculiarities of individual beings. Now it appears that such spontaneous tendencies are alone hereditary, and that whatever changes of organization are superinduced by external circumstances, and are foreign to the character of structure impressed upon the original stamina, cease with the individual, and have no influence on the race."

"Yet this law of hereditary conformation exists with a certain latitude or sphere of variety, but whatever varieties are produced in the race, have their beginning in the original structure of some particular ovum or germ, and not in any qualities superinduced by external causes in the progress of its development."

These sentences might well have been written to-day, to sum up the results of all our observations on such subjects. These results have been summed up at greater length and in more technical language, but I venture to think that Dr. Prichard's statement contains everything that is valuable and essential in every later attempt. It will be observed that Weismann's conception of inherent characters as blastogenic, acquired as somatogenic, stands out clear and distinct; furthermore, that the source of individual difference is traced to the germ.

After these general statements he returns to the question of disease and discusses predisposition. He points out that medical writers have generally believed that any predisposition to disease may arise in any constitution if subjected to

the appropriate causes; "that . . . the gouty diathesis, for example, may be acquired by long habits of intemperance, and transmitted to posterity," and so also with other ill effects witnessed in the children of dissolute parents. If this be so, Prichard admits that "we have a clear proof of the hereditary nature of acquired states of the constitution".

Against such a view he contends that any particular disease can only follow when there exists "a preparation, laid in the first place by nature, in the original stamina and habit of the body"; and he points out that the same hurtful cause may produce quite distinct diseases. Thus "intemperate living . . . is commonly said to bring on, in one person, a predisposition to gout, in another to diseases of the liver, or of the stomach, or of the brain. Now since the difference is not in the external causes, it must be in the natural peculiarities of the constitutions on which they act. These, therefore, are previously fitted by original organization to take on them one form of morbid affection rather than another. It is then clear that the predisposition is laid by natural or congenital structure, in the first instance." Individuals differ in particular organs; the exciting causes of disease bring out the weaknesses which previously existed and might otherwise have remained unknown. Such defects "being a part of the original bodily structure" are hereditary. "The first individual who exposes himself to the morbid causes, first betrays the peculiar defect of his race, and is thus erroneously supposed to lay the foundation for it."

Syphilis, which appears to be an exception, he explains by "a peculiar mode of infection. . . . This is evidently a phœnomenon of a very different kind from the similarity of structure which the laws of nature have ordained between parents and their offspring."

Hence he infers "that the phœnomena of predisposition to diseases, rather confirms than invalidates the general observations before laid down, and we may be allowed to conclude, that no acquired varieties of constitution become hereditary, or in any manner affect the race".

The preservation of complexion after a race has migrated to a very different climate conforms to the general law. Although the parents may alter greatly "the adventitious colour has no influence on the offspring".

Hence in looking for the causes of varieties of mankind we must not "direct our attention to the class of external powers which produce changes on individuals in their own persons, but to those more important causes, which acting on the parents, so influence them that they produce an offspring endowed with certain peculiar characters, which characters, according to the law of nature, become hereditary, and thus modify the race".

The sentence I have last quoted concludes the section and very naturally introduces section iv., entitled, "Theory of the Origin of Varieties" (p. 548).

This section opens with a sentence which might well have been written by Darwin: "Varieties of form or colour, as they spring up in any race, are commonly called accidental, a term only expressive of our ignorance as to the causes which give rise to them". On the other hand—"*how, by what influence*, and *in what manner*" they are produced, "we shall perhaps never be able to ascertain".

Examples of new varieties which have sprung up within the experience of man are then given: the "porcupine" and six-fingered man, albinos and variations in colour. He next describes the sudden origin of the ancon or otter breed of sheep, quoting from Col. Humphries in the *Philosophical Transactions* for 1813 (part i.).

Prichard favours the view that when the offspring does not exhibit a new variety but follows the main lines of its race or breed, it is apt to be influenced by the father rather than the mother; and he quotes a number of statements and opinions believed to favour this view; and finally alludes to the celebrated cross between the mare and the male quagga in which it was confidently believed that so great an effect was produced on the former that her later offspring, although begotten by a stallion, were influenced in the direction of the quagga (telegony).

The mother, on the other hand, was believed to be in

the main responsible for the new varieties which arise from time to time. This opinion Prichard considered to be probably well grounded; and the conclusion that size and stature chiefly depend on the mother he also thought to be well established. Hence we see that his judgment and penetration were not always proof against popular convictions insufficiently sustained by evidence. These strange views about the relative importance of the two parents seem to have disappeared, and only traces of them are to be found in the popular beliefs of the day.

The author dismisses the extreme cases of the supposed effect of the mother's imagination upon the unborn child as manifestly absurd; but looks with some favour upon the opinion, also held by Erasmus Darwin whom he quotes, that the future offspring may be effected by the imagination of the parent at the moment of conception. In proof of the ancient origin of this belief he alludes to Jacob's experiments upon the flocks of Laban.

When, however, Prichard comes to reconsider all his suggested causes of variation he is dissatisfied with them and admits that "the circumstances—are of a more permanent nature," and that it is often "impossible to discover any peculiar circumstance in the condition of the mother". This leads him to consider the similar instances among domestic animals and among plants and at this point he anticipates in a truly remarkable manner Darwin's general conclusions as to the origin of our domestic breeds.

"It is generally supposed," he says on page 557, "that cultivation is the most productive cause of varieties in the kind, both in the animal and vegetable kingdom. But it may be questioned, does cultivation actually give rise to entirely new varieties, or does it only foster and propagate those which have sprung up naturally, or as it is termed accidentally?

"In this latter way the influence of art is very important in constituting breeds, as of cattle, dogs, horses. The artificial process consists in a careful selection of those individual animals which happen to be possessed, in a greater degree than the generality, of any particular characters

which it is desirable to perpetuate. These are kept for the propagation of the stock, and a repeated attention is paid to the same circumstances, till, the effect continually increasing, a particular figure, colour, proportion of limbs, or any other attainable quality, is established in the race, and the uniformity of the breed is afterwards maintained by removing from it any new variety which may casually spring up in it."

The main result of Darwin's indefatigable labours on the formation of domestic races could not be more accurately summarised than in these words published in 1826.

Prichard expresses himself as uncertain whether domestic animals are more prone to vary than others, but considers that the artificial conditions may in all probability "occasion deviations in their progeny".

The influence of climate seemed to him the most important of all causes of race-formation—so important in fact that he discusses its examples under a separate section, while the adaptation of races, animal and human, to their climates form the subjects of the concluding sections vi. and vii.

The examples of the effect of climate are brought forward in section v. (p. 558), entitled, "Instances of Variety in the Breed, Arising from the Operation of External, Chiefly of Local Causes". The first instance is that of the swine of Cuba which are said to be twice the size of the parent breed. He then instances the peculiar and uniform colour of the cattle and horses "descended from the variegated domestic breeds" which have become wild in South America, and the common bear which differs in colour in various European localities.

When the races of several distinct species resemble each other in a single locality it is fairly maintained that some special local influence may be strongly inferred. Thus it is stated that the Angora breeds of rabbits, goats, and cats are remarkable for their long fine silky hair and white colour. "These characters . . . indicate a common cause, which must be some peculiarity in the circumstances under which these animals exist in the climate and situation occupied by them."

Then follow many other examples—the blackness which characterises both men and animals in Malabar and Guinea, the whiteness of Polar animals, the height of Patagonian man, the differences which separate the English race in America and the West Indian Islands from that in the parent country, and the negroes of America from those of Africa.

The section concludes in a significant paragraph in which the author suggests that perhaps some of these local varieties may be specially adapted to "the circumstances of the countries in which the deviation has taken rise," and he finally concludes by introducing the succeeding section in these words: "It may indeed be inquired, whether the deviations in general, which appear to follow a change of climate, are not founded on a law of the animal economy, which gives rise to an alteration in the breed calculated to fit the race for its new abode" (page 566).

The sixth section (p. 567) is headed "Adaptation of Certain Breeds to Particular Local Circumstances". In this section we are provided with numerous instances of the adaptation of races to their environments. Blumenbach's opinion in favour of the multiple origin of the dog is quoted at some length. Considering the undoubted adaptation of many breeds for certain ends this naturalist concludes: "I can scarcely persuade myself to look upon this as a mere accidental consequence of degeneration, and not rather as an intentional contrivance of the wise Creator". To this Prichard replies that such a remark "suggests the inquiry whether the degeneration or variation of animals is in fact a mere accidental phænomenon . . . ". We should note that degeneration is here used in the sense of departure from ancestral type, and not implying, as it does in our time, any degradation or simplification of structure.

Then follows a paragraph most significant of modern views of organic evolution and the kind of evidence on which the modern naturalist relies. The remarkable "double relation" which individual species bear on the one hand to their special localities, and on the other to the group to which they belong, is first pointed out, and main-

tained to be characteristic of the vegetable kingdom as well as the animal. Thus the species of a family or genus are often distributed round a centre "which seems to be the principal focus or favourite seat of the tribe," from which the branches diverge in various directions. The particular species, when compared, can be referred to "one type of organization". The slighter differences between them "seem to lose themselves in the sameness of form belonging to the genus, and even suggest a suspicion that they all proceeded from one original. The phænomena of resemblance must have had their sufficient reason as well as those of diversity." He then inquires whether the explanation is to be found in the action of "some slight modification in the productive causes" which stamped the genus at its first appearance "with all these specific diversities"; or whether on the other hand a uniform genus was first created which "afterwards became diversified by the influence of external agents". He concludes that the former of these alternatives is more strongly indicated by the knowledge of his time.

"Whichever of these suppositions may be true in point of fact, the separation of families and genera into particular species, and the distribution of these species to particular habitations, according to their physical properties, is evidently a part of the provision of nature for replenishing the earth with organized inhabitants, placed everywhere according to the congruity of soils and temperatures, with their structure and habitudes.

"But why is it to be supposed that the influence of this law of adaptation has stopped here? Is it not probable that the varieties which spring up within the limits of particular species, are further adaptations of structure to the circumstances under which the tribe is destined to exist? Varieties branch out from the common form of a species, just as the forms of species deviate from the common type of a genus. Why should the one class of phenomena be without end or utility, a mere effect of contingency or chance, more than the other?

"There are indeed many instances in which we can

perceive an advantage in the varieties of form, and an adaptation of particular breeds to external circumstances." He then gives numerous examples—the small active cattle and horses which are found in mountainous countries, the larger forms which flourish on fertile plains; the various breeds of the hog which are believed to hold "a particular relation to the localities in which they are placed"; the change of a thick fleece into a thin coat when certain breeds of sheep are transported to the tropics. "On considering these and analogous phenomena, we can scarcely avoid concluding that the variation of animals proceeds according to certain laws, by which the structure is adapted to the necessity of local circumstances."

This statement looks at first sight very much like natural selection. It is clear however that the writer held a view similar to that which has been termed "self-adaptation" by some modern writers, *viz.*, that external influences act on the organism in such a manner as to evoke directly a favourable response.

Examples of similar adaptation are then found among the races of man. The skin of black races is considered to be a protection against the effect of heat; the native African races can multiply in localities where a white population cannot maintain its numbers, while negroes are unable to establish themselves in northern latitudes. From these and many other instances, it appears that "in mankind, as in some other races, particular varieties are adapted by constitution and physical peculiarities to particular local situations".

The section finally concludes with the following paragraph: "These remarks, if they are well founded, serve to illustrate the doctrine of variation, or deviation, in the races of animals in general, and they seem to lead us to the conclusion, that this is not merely an accidental phænomenon, but a part of the provision of nature for furnishing to each region an appropriate stock of inhabitants, or for modifying the structure and constitution of species, in such a way as to produce races fitted for each mode and condition of existence. A great part of this plan of local adaptation appears to have been accomplished by the original modifi-

cation of a genus into a variety of species. It has been further continued, and the same end promoted, by the ramification of a species into several varieties."

The seventh and last section (p. 575) of this part of the work treats "Of the Relation of Particular Varieties of the Human Species to Climates".

Prichard evidently thought that adaptation of races to climate is especially characteristic of the human species, and must be admitted to hold in certain instances whatever be thought of his hypothesis that "the varieties in the species of animals proceed from a principle in nature, modifying the structure and constitution of races, and adapting them to the physical circumstances under which these races may be destined to exist . . .". He considers that the distribution of the races of men bears "a certain relation to climates," and gives a broad sketch of the geographical arrangement of races in support of this opinion. At the conclusion, after inquiring how it is that "these varieties are developed and preserved in connection with particular climates and differences of local situation," he gives the following very significant answer: "One cause which tends to maintain this relation is obvious. Individuals and families, and even whole colonies, perish and disappear in climates for which they are, by peculiarity of constitution, not adapted. Of this fact proofs have been already mentioned." We have here the undoubted recognition of natural selection, and it is remarkable that a man of such penetration who recognised fully that domestic breeds are due to man's selection, should not have seen in this principle a larger importance and have extended it to the relations of species to each other as well as to their physical environment. Great as Prichard was he did not appreciate the most pressing part of the "struggle for existence".

Prichard furthermore considers it probable that there are local influences which "promote the appearance of those varieties which are best suited to them, or tend to give rise to their production in the breed". He freely admits that this conclusion conflicts with his contention in section ii., that the colour of a race is not permanently

affected by a change of climate, and, he might have added, conflicts equally strongly with his argument in section iii., that acquired characters are not transmitted. However, he is so fascinated by the view of a local influence directly producing adaptation that he throws over much that he had previously argued for in a most convincing manner. Thus he suggests that races of men when removed into another climate may not change because they are defended from the local influences by living in houses, adhering to their old foods, etc., also that the facts about the black and white Jews of Cochin, from which he argued in section ii. that climate produces no permanent effect on the race, may be insufficiently known.

It is strange that one who reasoned so acutely in section iii. did not seem to see that the following view if proved to be true would undermine the whole of the argument: "It may however be true, that particular varieties, once established in the stock, and transmitted for many generations, though originally resulting in a certain degree from the influence of local causes, will nevertheless continue permanent, even long after the race has been removed from the climate in which they originated".

In spite of this logical flaw, which is in itself of much interest, inasmuch as it probably explains the suppression of Prichard's original views in later works, sufficient has been said to prove that the author was one of the most remarkable and clear-sighted of the predecessors of Darwin and Wallace.

E. B. POULTON.

X. *On the Courtship of certain European Acridiidæ.* By Professor Edward B. Poulton, M.A., F.R.S., F.L.S., etc.

[Read April 1st, 1896.]

The extraordinarily fine and hot weather in Switzerland at the end of August and beginning of September last year (1895), was very favourable for the observations which are here recorded. I was then staying at the Weisshorn Hotel, high above Vissoye, in the Val d'Anniviers, 7690 feet in elevation. Certain species of *Acridiidæ* were excessively abundant in the immediate neighbourhood of the hotel, species moreover which afforded examples of very different methods of courtship.

In working at this subject I received the greatest assistance from my two friends, Mr. F. Jenkinson and Mr. F. V. Dickins: their keen powers of observation enabled me to add many new facts of much interest, and also afforded valuable confirmation upon the most difficult points. Mr. Jenkinson observed with me for hours together on several occasions, so that we were able to compare our impressions as we received them.

Dr. Sharp has kindly identified the species for me, comparing my specimens with a Brunner collection at Cambridge.

The object of this enquiry was to make out the methods employed by the males in the courtship of the females, and especially the part played by stridulation. Dr. Sharp, in the Cambridge Natural History (Vol. v., p. 286), insists on the insufficiency of observations on this point, and I therefore hope that this work has not been in vain. The following observations suggest that the true significance of the latter is to be found in its use during courtship. In only a single species of those observed, *Stethophyma fuscum*, did the males commonly stridulate without reference to the females, and merely in rivalry with each other. In all the other sound-producing species the power seemed, almost without exception, to be

exercised with direct reference to females, or in rivalry to other males in the presence of a female. In the case of *Psophus stridulus,* true stridulation was only observed when the close proximity of a female had evidently thrown the male into a state of excitement.

The following considerations also support the same conclusions. In *Pezotettix pedestris,* both sexes have rudimentary wings and the male never makes any audible sound. Nevertheless, when he is seated on the back of the female attempting to pair, and during coitus itself, he continually moves his third legs alternately as if in stridulation. I believe that this movement is a vestige of an ancient and long-lost power of producing sound. Although stridulation is usually produced by a symmetrical movement of the third legs, it will be shown that this is not the case with *Stenobothrus elegans.* There is therefore no objection to be raised against this character of the movement in *Pezotettix.* Another view, and that held by my friend, the learned Orthopterist, Henri de Saussure, is that sound is really produced, only we cannot hear it. He holds that the sound is merely the outward expression of the elated feelings of the male *Pezotettix.*

Dr. Sharp, too, considers from the presence in apparently dumb species of well-developed tympana—and this is their condition in *Pezotettix*—"that the Orthoptera provided with acoustic organs, and which we consider dumb, are not really so, but produce sounds we cannot hear, and do so in some manner unknown to us" (Cambridge Natural History, Vol. v., 287). On the other hand, it may be urged that the perception of vibration by means of tympana may be of great value in the life of an organism, even if the organism were incapable of producing sounds, and that it may be retained for some more general use when its original special function has ceased to exist.

But in any case this movement of *Pezotettix* is conducted with an apparatus homologous with that by which sound is produced in other *Acridiidæ,* and yet one in which the special sound-producing structures are absent. The tegmina are too short to be brought into their usual relation with the femora, and the ridge on the inner face of the latter is without the "musical beads," although strongly chitinized and prominent as though it had previously possessed significance in this respect.

Further evidence in support of this explanation is to be found in the fact that *Pezotettix* makes the movement when he has succeeded in capturing the female and when pairing has actually begun. In the other species observed the normal arrangement was for the male to stridulate apparently to charm or please the female *before* leaping on her; stridulation after this occurring only in certain special cases (one observation on *Stenobothrus hæmorrhoidalis,* and one on *Stethophyma fuscum,* in which it is to be explained as an answer to another very persistent male).

If, however, as I suppose, the movements of *Pezotettix* are merely vestigial, we can quite understand their association in the nervous system with those stronger nervous impulses which are concerned with the successful issue of courtship, rather than with the impulses concerned with courtship itself. According to this view the functional stridulation is associated with anticipation while the vestigial stridulation is only evoked by realization. It should be added that it is quite possible that these movements of the male *Pezotettix* may have a stimulating or perhaps merely a soothing effect on the female.

The comparison between *Pezotettix* and the other species supports in another way these conclusions as to the essential significance of stridulation in courtship. In the latter kinds, so far as they were sufficiently observed, the female was treated with considerable ceremony; in *Gomphocerus* a peculiar attitude was assumed, movement of some of the appendages of the head was made, and the female was in some cases patted or stroked, in addition to the most assiduous stridulation. The latter was never omitted in any species in which we could detect any sound. But the little male of *Pezotettix,* being apparently without any power of charming the female, behaves in a manner entirely different from any of the others described below. He lies in wait, leaps on the female, and captures her unawares. Then, when he is firmly seated, the male attempts to charm her by nibbling with his mandibles, and perhaps by the effect of the alternate movement of his third legs.

The general impression left by the whole of the observations recorded below was favourable to the theory of sexual selection, and to the view that the stridulating

apparatus has been evolved by the agency of this principle rather than by that of natural selection.

Others may draw opposite conclusions from the same observations, which I therefore set forth by themselves, apart from general theoretical considerations. I believe that the observations themselves are correct, and that the uncertain points are stated with due caution.

Pezotettix pedestris.

August 29, 1895.—I watched a pair of *Pezotettix pedestris* continuously for about an hour and a quarter, viz., from about 2.30 p.m. to 3.45. The day was fine and the sun powerful, and this had been the case for many days previous to the 29th.

When first observed, the male was seated on the back of the female, the anterior legs being clasped round her prothorax, but every now and then one of them was passed round her head and sometimes even over the eye. Twice the female was seen to raise her leg and sweep the male's leg off her face. The male's second pair of legs apparently clasped the posterior part of her first abdominal segment, fitting in between the femora of the female's third pair of legs and her body. The male's third pair of legs were not used for maintaining his position, but were held either horizontally or inclining upwards posteriorly, the tibiæ forming an acute angle with the femora, and the tarsus being raised so as to form an acute angle with the tibiæ. For nearly the whole of the time of observation the male's third legs were jerked up and down alternately, the strokes not succeeding each other very rapidly. No audible sound was produced. No corresponding movement was seen on the part of the female.

In attempting to copulate, the male let himself down, sometimes on one side and sometimes on the other, sufficiently far to bring the extremity of the abdomen below that of the female. The terminal segments of the male's abdomen were then turned upwards and inwards towards the external generative aperture of the female, with which the everted male organs were brought into contact. No movement of the corresponding female parts was seen, but contractions of the whole abdomen occasionally took

place. In the above-described attitude the hold of the male appeared to be very precarious, and it seemed that he would have been shaken off by a comparatively slight movement on the part of the female.

During the second half of the period of observation, the male made more frequent and vigorous attempts, and I noticed that from time to time he gently nibbled the female with his mandibles in the dorsal and upper part of the lateral thoracic regions. The female, however, appeared to be entirely indifferent to his attentions; and sometimes when the male was making the most energetic attempts she would calmly begin to eat the leaf of a plant. On two occasions she finished, or nearly finished, a small leaf, and many times nibbled parts of leaves. Although she seemed to prefer the green leaves, she sometimes ate portions of brown ones. Five times the female ejected fæces; once I thought the male did so, but it may merely have been getting rid of some foreign particle which had accidentally adhered. In the case of the female there was no doubt.

Although the female did not attempt to get rid of the male, she showed her indifference to his presence not only in the manner already described, but by walking and hopping about, often at the most inconvenient times. By 3.45 copulation had not commenced, and I could wait no longer. Both insects were then captured for identification.

All the observations recorded above were made quite close to the insects. By keeping as still as possible, and moving very gently when it was necessary to follow them, it was easy to bring the eyes within six or eight inches of the insects without disturbing them at all.

August 30.—I saw many of the same species in copula beside the upper road, or rather path, leading from the Weisshorn Hotel to Zinal. The terminal segments of the male's abdomen are turned upwards, in the position indicated by the attempts already described. The alternate movements of the third legs continue from time to time during coitus: in one case (which may have been the beginning of copulation) a female was seen to stretch out the third legs from time to time, and make a rapid shivering movement. With the above exception, the female hopped and walked about freely during the pro-

cess, the male being apparently firmly seated on her back.

August 31.—A pair were found in copula in the Alpine garden close to the Weisshorn Hotel. The female was seen to eat freely, and once to void excreta, while the male was actively moving his third legs. This observation was confirmed by F. Jenkinson. These remarkable alternate movements of the male's third legs during coitus were also seen by F. Jenkinson and me in a very large number of cases at other times. In a single case observed by F. Jenkinson on August 31, the male's legs were at one time rapidly vibrated laterally, being moved simultaneously and not alternately, as in the usual movement. This perhaps corresponds to the shivering movement seen by me in the female on August 30th.

September 1.—This latter observation was confirmed by me in the Alpine garden. In this case the beginning of the act was seen. The male appeared to be much excited, and the shivering movement occurred from time to time, just before and after the beginning of the act. The female, which possessed only one leg of the third pair, was quite motionless throughout. At the commencement of the act she expelled fæces, which were moist and quite different from the dry ejecta seen on other occasions. In this and the complete passivity of the female there is probable evidence that she was much influenced by the act. This passive appearance was entirely distinct from the indifference manifested in so many of the cases previously observed, in which, however, the act had either not begun, or was probably far advanced. Shortly after coitus the pair remained motionless for a considerable time.

September 2.—Up to this date the events immediately preceding pairing, and the pairing itself had been observed with care, but there was no evidence to show how the male became seated on the back of the female. I was very anxious to find out how this occurred, and whether there was any preliminary courtship by stridulation or otherwise, although the species had never been heard to stridulate. At this date, F. Jenkinson observed, and I was able to confirm, that the males leap upon the females when they come within a distance of about three inches, but apparently do not notice them at a much greater distance. Their attention appears to be directed to the

female by its movement, and they then leap with the greatest accuracy F. Jenkinson obtained these results by inducing captured females to leap from his hand in the direction of a male. On one occasion he saw a male approach and leap upon another male, probably mistaking it for a female; there was a tussle, in which one appeared to try to bite the other. It thus appeared evident that there is no preliminary courtship of any kind, but that the male takes the female by surprise, and leaps upon her before she is aware of his presence. This conclusion was abundantly confirmed later on.

SEPTEMBER 3.—F. Jenkinson and I observed a pair on the grassy slopes below the Bella Tola. The male had lost one of the legs of the third pair, and the female had one of them apparently injured. The male was seated on the back of the female, and was energetically attempting to copulate much too far forward in the middle ventral line. We watched his continual attempts for about fifteen minutes, at the end of which period he was no nearer to success than at the beginning. This failure, when the female was evidently ready, and kept opening the generative orifice, may have been due to the absence of the leg. Although this limb is not used to hold firmly, the absence of it may have affected his balance. At any rate no failure of this kind was seen on any other occasion.

Later on, about the middle of the day, we came to a flat piece of ground covered with scanty grass, at the bottom of the zigzags by which the Bella Tola is ascended. The strong sun and the position of the ground made the place extremely hot, and as both sexes of the *Pezotettix* were very abundant, it appeared a good opportunity for observing the pairing habits. The males were often seated on stones, or other slight eminences; thus placed, and with the head and anterior part of the body raised, they were in a very favourable position to see and leap upon any female which approached within three inches, or sometimes even a greater distance. If the leap is a failure, the male at once begins an active pursuit, leaping more quickly and further than the female. In this way it often happens that he loses sight of the latter, or, is brought nearer to another female, whom he at once attempts to capture. One main cause of failure in the pursuit is that the male has very little, if any, power of

seeing a female between his leaps, unless his attention has been directed to her by the movement of the leap itself. Hence the pauses, often greatly prolonged, between the successive leaps frequently lead to the escape of the female. Furthermore, the leaps made by the male, when lying in wait for the female, were much better aimed than those made in pursuit. It is probable that in the former case he takes very careful aim; for he turns his head and antennæ in the exact direction of the female, and pauses before leaping, often making a slight rocking movement of the anterior part of the body. Occasionally this movement was seen in the female also.

When the male leaps upon her unawares, as I have described, the female almost invariably tries to throw him off, and generally succeeds. If, however, she failed in the first attempt, in most cases she yielded forthwith, and, probably as a result of these favourable conditions as regards temperature, pairing was effected in a very short time, sometimes even in a few seconds.

In one instance a male leaped upon a female and was thrown off; the female was then driven round, so that in a few minutes she again came within the range of his leap. The second time he was successful, securing a firm hold, and beginning to nibble the female with his mandibles. All resistance ceased, and pairing took place in a few minutes.

Very occasionally the alternate strokes, but only once or twice repeated, of the male's third legs were seen when the opposite sexes were near together. I believe, too, that the same movement was made by the female, though still more rarely. One female, when near to a male, seemed to be excited, and raised her third legs, which quivered from time to time. Any such indications were very rare in the female. In nearly all cases she was taken by surprise, and only yielded when very firmly held.

The female must be influenced in some way by the male holding her and caressing her with his mandibles; for his position, when attempting to copulate, is very precarious, and he could be easily shaken off. It appeared, however, that the males did not begin to make any such attempts until the females had ceased to resist.

In one single instance the female did not yield, although very firmly held; but it is probable that she was immature, or injured, or in some way unfit for pair-

ing, as the male finally left her of his own accord. This observation was made by both of us, and was of great interest. When we first saw them, the male was firmly holding the female, but she kept struggling violently, and trying to kick him off with her powerful third legs. On at least three separate occasions the pair rolled over, and remained in this position, with the male beneath, for about half a minute. At such times the female was unable to struggle at all successfully, and it seemed possible that the male, when he was nearly unseated, caused the pair to roll over; we could not, however, be sure of this. Ultimately the male leaped off voluntarily, as I have already stated. One side of the dorsal surface of an abdominal segment was wounded in the female, but as the injury did not appear to be fresh, it is not probable that the male caused it.

In one or two cases the female, and once the male, expelled fæces just before or during copulation. The fæces were of the character already described, and not in the usual dry state.

In no single case was any preliminary courtship witnessed in this species. There was no stridulation, no display of colour or attitude. It was entirely a question of capture, the females being almost invariably, at any rate at first, unwilling prisoners, although occasionally they showed indications of excitement in the presence of a male.

It is highly probable that pairing takes place many times in this species, and even more than once with the same male.

There was an extremely high proportion of individuals in coitu, even allowing for the fact that their habit of freely jumping about renders them much more conspicuous than the unpaired males and females. The proportion was far higher than that of any other Orthopterous insect observed during this visit to Switzerland; it is possible, however, that the principal pairing time of other species is earlier in the year.

Gomphocerus sibericus (var.).

This form was excessively abundant round the Weisshorn Hotel, no other species approaching it in numbers. On one occasion, after heavy rain, F. Jenkinson saw immense

numbers of them lying in the path apparently dead; but after the sun had warmed them they all recovered.

August 30.—At this date I had a good opportunity of watching the habits of the males in the presence of a female. About a mile from the hotel, along the upper road to Zinal, at about 11 a.m., I came upon a spot which, on account of its aspect and slope, had not long been warmed by the sun, so that the insects were only just beginning to bestir themselves. Here was a little group of this species—two males and a female—probably close to the place in which they had passed the night. The female was resting quietly on a small piece of rock, slightly moving her abdomen, probably in relation to respiration. Later on she drew each antenna beneath the first leg of the same side, or perhaps drew the leg over the antenna. It is probable that this movement is intended to wipe off the dew. The males often did the same, and the female rubbed its eye, probably for the same purpose. This explanation is all the more probable because I did not see these movements at any time when the heat of the sun was sufficient to have dispersed the dew; although the species was carefully observed on many occasions. One male, standing by the female, was stridulating when I came up; the other was behind motionless. These three insects were extremely shy, although this was by no means the case at other times when individuals of this species were watched in the heat of the day. Although I approached so that my shadow was behind me, and very gently, the male beside the female was alarmed at each slight rustle or movement, raising himself on his legs and erecting his antennæ, apparently thoroughly on the alert. Then when I kept perfectly still he resumed his former position and depressed the antennæ towards the female, both of whose antennæ were also generally depressed. He did not continue to stridulate, but, after remaining almost motionless for some ten minutes, except for cleaning his antennæ now and then, turned his back on the female and apparently began eating the heather. In a few seconds the other male stridulated once or twice: the effect on the first male was instantaneous; he stridulated for a second or two and then walked back to the female, depressed one antennæ towards her and patted her on the thorax with one of the first pair of legs. After all this

attention she made no apparent movement, and the other male did not make any further advances. The active male then walked away and met another female, stridulated beside her until she also walked off. Another male close at hand stridulated, and the active one immediately replied, although in this case no female was near.

These observations illustrate the habits of the species in courtship, the males, as Mr. F. V. Dickins also pointed out to me, always running after the females and never jumping, although both sexes jump very actively when disturbed. The use of stridulation as one of the tactics of courtship was clearly seen, the rivalry between the two males near the female being particularly interesting. The same occasion gave rise to the other method of courtship, viz., patting the female. The position of the male's antennæ suggested attention to any movement the female might make, or to anything she might do.

These notes also illustrate the immense abundance of the species, the active male had only to walk two or three inches away from the group of three in order to come across another female and male.

I think that, in observations of this kind, it will be useful to watch the species under many different conditions, especially as regards temperature. In the hottest places courtship is most energetic, and we have the most favourable opportunity for seeing the whole process carried through to completion, as in the case of *Pezotettix* already described; but when the temperature is lower, and especially when the warmth of the sun has only just roused the insects into activity, many interesting details may be witnessed which are often passed over or hurried through in times of greater energy.

In spite of the excessive abundance of the species and the almost constant attention of the males to the females, a successful termination to courtship was witnessed in no single instance, and only two or three pairs were seen in coitu. One of these was found on August 29th, a little below the hotel. The male, unlike the *Pezotettix*, was unable to retain his hold, and when the female jumped, as she did freely, he was dragged along on his back, and retained this position for a considerable time in the intervals between two successive jumps. It is probable that with this species, the pairing season was nearly over;

and this conclusion is supported by the fact that the females were often seen engaged in oviposition.

August 31.—Jenkinson and I watched several females ovipositing in the loose earth on a very hot slope just outside the hotel, and in the beds of the little Alpine garden. The female thrusts her abdomen deeply into the earth and remains in this position for some minutes. On two occasions a female, after withdrawing her abdomen, was seen to rake the ground vigorously with her third legs, and, in one case, witnessed by Jenkinson, she steadied herself by holding a plant stem with her mandibles. We several times dug up the earth and searched for the eggs, but without success. At this date I found another pair of this species in coitu, on the path just below the hotel.

Gomphocerus sibericus appears to be a very general feeder, and its extraordinary abundance in the immediate proximity of the hotel was probably due to the presence of horses' and mules' dung, and other refuse upon which they fed. Every patch of dung upon the path was surrounded by dozens of individuals.

August 31.—F. Jenkinson and I watched the males pursuing the females near the hotel. It often happened that when a male came up to a female he extended the maxillary and labial palpi towards her, and raised himself on his legs in a very characteristic and remarkable attitude. At other times these movements occurred at a later stage of courtship. The movement of the palpi strongly suggested their use as organs of sense. When the female ran away, as she generally did, the male pursued, always trying to get in front of the female and thus stop her. The male ran faster than the female, and altered his direction so as to approach the female almost at right angles to the course she was pursuing. After the preliminaries of courtship—pursuit, stridulation, attitude, and movement of the palpi—the male, standing beside and close to the female, tries to jump on her, making a curious short chirp as he does so. The attempts were, however, always unsuccessful in the cases observed by us. Stridulation is in this species of definite length, and ends in two or three short chirps; in most cases the male then instantly approaches still nearer and tries to jump on the female with the short chirp already described.

Neither Jenkinson nor I can remember the exact

order in which the male went through the various phases of courtship. It is probable that the order varied greatly, and that some of the phases were often omitted.

September 2.—On this and many other occasions the males were often seen to leave the female they were pursuing and, apparently without knowing it, to follow some other female they accidentally came upon in the course of the pursuit. A male pursuing a female was once seen to approach and jump at the male of *Pezotettix*, having apparently mistaken it for the female.

September 3.—On the grassy slopes below the Bella Tola, a male observed by F. Jenkinson and me was greatly excited by the pair of *Pezotettix* already described as attempting, but unable to copulate. He stood in the characteristic attitude, walked round them, and finally stood in front and stridulated for the usual length of time and with the usual ending, he then advanced as if to jump, but before doing so became satisfied that he had made a mistake, and walked away. It was evident that he had mistaken the pair for the female of his own species.

Just below the zigzags up the Bella Tola we saw a male which, standing by a female, repeated the stridulation four times with the usual conclusion on each occasion, and then after all this attention let her walk away unperceived. This and the other facts already described seem to show that the males were very unobservant. In this respect their behaviour was very different from that of *Pezotettix*, and from the very alert member of their own species observed on August 30.

No light was thrown upon the function of the remarkable dilated tibiæ of the first legs of the male. The whole tibia, swollen into the shape of a pear, with the tarsus articulated to its broader end, presented a most curious appearance in the characteristic attitudes assumed during courtship. On the underside of this dilated mass, which is approximately circular in transverse section, two rows of hairs are seen. Although the hairs are smaller, and the rows more widely separated, both evidently correspond to those which are found beneath the unmodified tibiæ of the other legs.

Although we observed the habits of this species on many other occasions, neither F. Jenkinson nor I had ever seen the pairing accomplished. I therefore asked Mr. F. V. Dickins if he would consent to watch through

a very hot afternoon. This he very kindly did, and although unsuccessful in this respect, he made many interesting observations which I give in his own words:—

"On the 4th September, 1895, I watched the courting habits of some grasshoppers on the knoll immediately behind the Weisshorn Hotel.

"At first I made my observations on the west slope, but there was a cool wind blowing, and the insects were neither numerous nor lively. Casting about I discovered on the south-east slope a particular hollow away from the wind, in the full glare of the sun, and focussing the heat-reflections from the hillock-slopes around it. Here the grasshoppers abounded and were very lively; I watched them for about two hours.

"I noticed that the males, marked by swellings on their first legs, were much more mobile than the females, the latter were mostly extremely passive and had to be chased and caught up by the males. There was a good deal of this chasing which was very amusing to watch. Sometimes the female, as if bothered, would remain quiet for a time and allow the male to come up to her. He appeared to stroke her with his antennæ, but I could not distinctly see what parts of her body he thus specially caressed. The insects never seemed to leap unless alarmed; I thought that perhaps leaping was not an ordinary mode of progression. I saw no male clasp or leap upon any female; they chased and chased, threw up the game, started a fresh pursuit, equally bootless, and so went on, tireless. I was not fortunate enough to see any *accouplement*. When the male was alongside the female, in many cases, the insect assumed a strained attitude, the anterior part of the body being raised high, and the terminal segments curved upwards so that the dorsal line was concave antero-posteriorly. Very often a curious little click was heard, I thought, usually as the chase ended in the pair suddenly standing still by each other. One might suppose that it was a chirp of triumph. I have no doubt it was made by the male.

"One rather curious situation in this active little drama is worth noting. A female alighted or rather ran up on my boot and sat quite still in the hot rays of the sun. She sat so still that the idea struck me I might try to caress her a little myself. I accordingly looked round for a slender flexible grass stem or dried haulm,

and having found one gently touched her with the pliant extremity. She did not stir, and I became bolder; I rubbed her body on either side and also the inside of the coxæ and antennæ. She was still unmoved, except that a slight rigidity seemed to supervene, and the abdominal extremity curved slightly upwards. Gently tickling this part the curve rose and the rigidity seemed more marked. I now stroked her as gently as I could, and she permitted this extreme familiarity without resentment. Lastly, I took her softly up and laid her in the palm of my hand. Turning her from side to side she seemed quite content and did not exhibit a flutter or a tremor. I continued my caressings for ten minutes or a quarter of an hour, and then laid her in a warm spot and watched her for another quarter of an hour. She did not move, although she was alive enough. Was she hypnotized?"

This last interesting observation suggests that very marked effects may be produced by the patting which I witnessed on August 30th, and by the nibbling in the case of *Pezotettix*. In this latter species, indeed, the effect produced on a female after her first unsuccessful attempts to throw off the male, appeared to be very much like that induced by Mr. Dickins in the female of *Gomphocerus*.

Stethophyma fuscum.

This magnificent species was very abundant in the open grassy spaces between the trees at the water-courses some few hundred feet below the hotel, and also in certain places on the slopes far below the Bella Tola. The stridulation was far more characteristic than that of any other species observed: first three (sometimes two) strokes of the third legs across the tegmina, then a rapid vibration of the former against the latter for a few seconds. The result is three piercing sounds in rapid succession, and then a prolonged rustle. The rivalry between the males and their replies one to another were very evident, but their relations to the female were only witnessed once or twice.

August 31.—This species was observed by the water-courses. Many females were seen but never attended by males on this occasion. I came across a pair of males in the grass fighting in a very clumsy manner: they lay

side by side, pushing and kicking at each other, and stridulating alternately. One male had lost one of the third pair of legs, perhaps in an earlier part of the fight, but if so it must have been somewhere else, as I searched for the leg in vain. In spite of its mutilation it replied with its single leg to every stridulation made by the other, and these replies seemed especially irritating to the uninjured male for it kicked more vigorously than ever, and once made a determined but unsuccessful effort to bite the end of the other's abdomen. The fight was already raging when I began to observe. After I had watched it for several minutes the uninjured male gave up and went away. It is possible that the fight may have begun by one male leaping on the other in mistake for a female, but it is more likely that it arose in a quarrel over one female. This view derives some support from the following observation.

SEPTEMBER 2.—At a certain spot on the slopes below the Bella Tola the species was very common, and several pairs were seen in coitu. The female is larger and duller in colour than the males, and her wings are much smaller and probably useless for flight.

In the case of one pair in which copulation had evidently only just taken place, the female was seen to expel fæces: another male was lying beside the pair evidently trying to copulate with the female, continually stretching his abdomen towards her with partial eversion of the organs. He also stridulated from time to time, and I feel almost sure, although I cannot speak with certainty on this point, that the copulating male replied on each occasion. In a few minutes the unsuccessful male went away. I have suggested that the fight may have begun in some such contest, but probably before either male had succeeded in pairing. I cannot now remember whether the stridulation during the fight and on the occasion last described was similar to that which is characteristic of the species at other times. I am confident that no new sound was introduced, but cannot be sure as to whether both movements were made with their usual relation to each other.

SEPTEMBER 7.—F. Jenkinson saw two males of this species drawn together from a distance of several yards apparently as the result of stridulating alternately. When at length they met, they seemed much excited,

but soon separated without fighting. Perhaps the fight which I witnessed may have begun in this way.

STENOBOTHRUS (?) ELEGANS.

A beautiful little species which Dr. Sharp doubtfully identifies as *Stenobothrus elegans,* was often seen, although not abundant, below the hotel. The males in stridulating, do not, like the two last mentioned species, move the third legs symmetrically, but one follows the other. Probably in consequence of this the sound swells and diminishes rhythmically, presenting a remarkable likeness to that made by a fly caught in a spider's web. Considering its very small volume, this high and piercing sound can be heard for a great distance.

STENOBOTHRUS HÆMORRHOIDALIS.

After I left, F. Jenkinson observed a very small kind which is almost certainly to be identified as the above named species. Mr. Jenkinson has kindly given me the following notes:—

"SEPTEMBER 5.—About 5 p.m. I found a very small brown male, with the dorsal surface of the abdomen of a reddish-orange colour. He was very assiduous in his attentions to a green female with white V-shaped marks on the side of the thorax. He generally kept close to her, but was never obtrusive in his attentions, relying apparently on the effect of his stridulation. This was made with both legs simultaneously, generally very low, but sometimes louder, a rapid uniform trill, rather like the note of the lesser whitethroat. Sometimes she gave him the slip, and they were as much as eight inches apart, and out of sight of each other; but he continued at short intervals his stridulation, and somehow, *apparently* by accident, they came across each other again, and the male posted himself in close attendance as before. The female was generally nibbling at blades of grass. If the male touched her, she seemed to repel him by raising one of the third pair of legs. At 6·45 the sun was setting, and I had to go, so I boxed them both. The male was perhaps just beginning to relax his energy.

"SEPTEMBER 7.—Below Weisshorn Hotel. A male was stridulating and following a female, and was more

successful in finding her again than any other species I have observed. At 5·30 the male jumped on the posterior part of the female's body, his legs round her tegmina. In this position he continued to stridulate although at rare intervals (he did so at 5·50). The female carrying the male shifted backwards moving her abdomen. She seemed to have some difficulty in expelling fæces, and this was apparently the cause of the movement. The male stridulated, and then at 6·0, without having copulated, he quitted the female, stridulated, and went away."

Psophus stridulus.

The large black males were common just below the hotel, and on some slopes below the Bella Tola, where *Stethophyma fuscum* abounded. Their red under wings were very conspicuous when flying, the characteristic rattling sound still further attracting attention to them. The larger brown, toad-like females, with smaller wings, are probably unable to fly.

I never saw the sexes together; but after I had left, F. Jenkinson kindly sent me the following notes :—

" September 5.—When the male finds himself near a female, he utters a double 'twitter' (once a twitter and then a trill), and moves excitedly. In one case I saw him leap on the back of a female, but presently he left her of his own accord.

" At 3 p.m. I came across a pair in coitu, but the male disengaged himself by vigorous movements of the third legs. They remained for a long time within two inches of each other, but nothing happened. I made the female jump away, caught her, and put her in the male's way. He at once became excited, and twittered, but the female escaped. This occurred more than once, when I lost her.

" A male, disturbed as I came home (about 6·45 p.m., when the sun was setting), hopped vigorously, but did not open his wings." This latter observation is of interest, because the males always took to flight, when disturbed, on other occasions.

" September 7.—On placing the female near the male, he became excited, and made a twittering sound with his legs. The female, in moving off, showed the red

under wings, but even in the open path, the male seemed to lose her at once. In another case, when the female came near, the male jumped right away."

It is noteworthy that most of the observations upon the last-named two species were made late in the afternoon, when the sun was losing its power.

Œdipoda cœrulescens.

I had long wished to study the courtship of these beautiful insects, but there were none round the Weisshorn Hotel. Lower, at San Luc (5390 feet), they began to appear, and still lower, at Vissoye (4006 feet), and all along the main valley road, they were excessively abundant. They are always difficult to observe, because they haunt places where the combination of direct heat with that reflected from rocks or bare slopes, is almost unbearable. I had no time to observe them until we had come down to Fribourg.

September 9.—These insects were very abundant in a large gravel pit, just outside the gate of the town, on the road to La Roche. There is little doubt that they belonged to the above-named species. They were very lively, continually flitting about over the bare earth and gravel. They are very shy, and it is necessary to keep perfectly still in the intolerable heat, in order to watch their habits. I noticed that the males move their third legs as if in stridulation, but that no audible sound was emitted. There is an apparent lack of intention and effort about their movement which suggested that the habit is probably only a vestige, and possesses no other significance. The legs were raised, and seemed to be allowed to drop by their own weight. Furthermore, these strokes were not repeated at regular intervals, but quite irregularly, and often singly. In this case I did not secure any material, and therefore cannot speak with any confidence; but I anticipate that the legs will be found to be without the sound-producing structures.

A female remained motionless on the ground near to me. She was much larger than the males, and the exposed surface of her body and wings was of a redder brown. The males were extremely acute in detecting her presence, although she made no movement, and looked exactly like a part of the ground. Whenever a

male perceived her, he instantly approached without any preliminary courtship, leaped upon her back, remained a few seconds, and then voluntarily left her. The female did not make any apparent movement, although I saw quite half-a-dozen males leap upon her in the course of a few minutes. The males never met near her, and I saw no signs of any fighting. I could not tell whether there was any actual pairing, but it is improbable that this could have occurred in so short a time. It is likely that the males found that she was in some way unfit for pairing, and then left her. I have already implied that there was no special display of the beautiful blue under wings for the benefit of the female.

I trust that I may be able to make further observations upon these beautiful and interesting insects at some later date.

[*From the* Proceedings of the Royal Society, Vol. 54.]

5

"The Experimental Proof that the Colours of certain Lepidopterous Larvæ are largely due to modified Plant Pigments derived from Food." By Edward B. Poulton, M.A., F.R.S.

Received May 12,—Read June 8, 1893.

[Plates 3 and 4.]

In a paper printed in the 'Proceedings of the Royal Society' for 1885 (pp. 269—315), I brought forward many reasons for regarding certain elements of the colouring of Lepidopterous larvæ as modified chlorophyll derived from the food plant. For this altered pigment the name metachlorophyll was suggested (*loc. cit.*, p. 270). Many other observations, subsequently made, supported the same conclusion; but it was not until the summer of last year (1892) that I was able successfully to carry out the critical experiment, viz., selecting a species of larva which normally eats green leaves, to feed it from the egg upon parts of the plant from which all colouring matter is absent.

This experiment was carried out in the following manner:—

A captured female of *Tryphœna pronuba* laid many hundreds of eggs in a chip box. The first larvæ began to appear September 7, 1893. On this and the subsequent dates, the larvæ intended for the purposes of these experiments were arranged in three sets, fed respectively upon—(1) the yellow etiolated leaves from the central part of the heart of the cabbage, (2) the white mid-ribs of such leaves from which the yellow blade was carefully removed with scissors, (3) the deep green external leaves of the same plant.

In all other essential respects the conditions of the three sets were the same. All were kept in the dark to prevent the change of the etiolin into chlorophyll. They were only exposed to light during the times necessary for comparison and feeding, and these are indicated below. A few were kept in glass cylinders standing on plates, the majority being confined in white earthenware pots covered at first with white muslin, but subsequently with glass sheets. Eventually all were kept in pots.

It is clear that the only essential difference between the conditions of the sets was the fact that the food of the first contained etiolin but

no chlorophyll, while the food of the second contained only a little etiolin, and that so situated (around the fibrovascular bundles and buried deeply in the substance of the mid-ribs) that the larvæ could not make use of it, while the food of the third contained abundant chlorophyll.

It is evident that any constant difference between the larval colours in the three sets followed from these differences in the food supplied them; and, unless there are reasons for believing that the differences were due to pathological change, and thus an *indirect* result of the food, we must hold that they are a *direct* result, and that important elements of the larval colouring are dependent on the existence of some modification of pigments derived from their food.

The course of the experiment will now be described in a tabular form.

Dates.	(1) Etiolated leaves.	(2) White mid-ribs.	(3) Green leaves.
Sept. 7	18 larvæ, the first to hatch, introduced.		
Sept. 8	45 larvæ added.	About 50 larvæ introduced into 2 pots.	75 eggs, from which the larvæ were hatching, introduced.
Sept. 22	Re-fed; 40 placed in a cylinder and about 18 in a pot.	Re-fed; about 20 alive in each pot.	Re-fed; about 30 larvæ counted.
Sept. 27	Length about 8·5 mm. Some of these larvæ were distinctly, although rather faintly, green. 20 removed from cylinder into new pot.	All white, with no greenish tinge. 10 removed and placed in a bottle, and 10 in a new pot.	Re-fed; 28 or 29 counted.
Oct. 4	The longest larva 15·75 mm. long when extended in walking. Many changing skin. The black subdorsal semilunar marks distinct in many of the largest. Most were pale, but distinctly green, and all apparently with *some* green shade; very different from the pale yellow colour of the etiolated leaves. The larvæ remaining in cylinder were now placed in a pot.	Again re-arranged: 9 placed in one pot, 9 in another, and 11 of the smallest in a third.	28 counted; 1 killed accidentally; 13 placed in one pot, and 14 in another.
Oct. 10	All very carefully compared. 27 in 4th stage, very uniformly about 23·0 mm. long, when fairly extended at rest; 5 *pale distinct green*; 12 *dark greenish*, varying according to the amount of dark superficial pigment, and transitional into	24 alive. Again re-arranged in 4 groups, placed in separate pots, containing respectively the 5 largest, the 9 next in size, the 5 next in size, and the 5 smallest. The largest were in 2nd stage. All quite white, being quite as large as those fed	These larvæ were frequently compared together and with those of experiment (1). There was no essential difference, except that these grew rather more slowly. At this time they were similarly

Dates.	(1) Etiolated leaves.	(2) White mid-ribs.	(3) Green leaves.
	the *brown* larvæ (10) in which the green colour is absent. The palest green larva, a similar larva with more superficial pigment, a typical dark greenish, and a typical brown larva were selected for painting at this date, together with a *very* deep bluish-green larva, which changed its 3rd skin just before being painted (see Pl. 3, fig. 1). The shade of green was far deeper than in any other individual. 11 larvæ in 3rd stage, the largest being 18—19 mm. long when extended. 7 *pale green*, 1 *pale brown*, 3 *deep brown*. 23 larvæ changing 3rd skin. 13 *pale green*, 5 *darkish green*, including the deep bluish-green one represented in fig. 1, Pl. 3 (4 of these changed their skins during the comparison), 6 *brown* (2 being greenish and transitional).	upon etiolin (1) on Sept. 27, when they began to become green.	green and brown of various shades, darkening, as they entered the last stage, into brown.
Oct. 11		3 of the largest were figured (see Pl. 3, fig. 2). They were in the 2nd stage.	
Oct. 19	The larvæ had grown rapidly, and a few had entered the last stage, while several were changing the last skin. As they matured they became darker, and all	5 largest were all about 11 mm. long when extended; 3 were changing 2nd skin, 2 large in 2nd stage. Same white appearance with faint greyish shade, due to	

Dates.	(1) Etiolated leaves.	(2) White mid-ribs.	(3) Green leaves.
	eventually turned brown, mostly of a dark shade.	superficial true pigment. Of the 9 next in size 3 were dead, and the 5 smallest were all dead or dying.	
Oct. 26	Nearly all in last stage, and brown of various shades, occasionally faintly greenish.	The 2 largest were 12·0 and 13·5 mm. long respectively when extended. Of the 6 next in size 2 were dead, and of the remaining 5, 2 were dying.	
Oct. 29		Of the 5 largest, 4 were dead by this date or in the course of the next day or two. The remaining larva was placed (Oct. 29) on etiolated leaves.	
Nov. 2	Mostly mature, and various shades of brown. When carefully compared with the larvæ fed on green leaves (3) no difference in colour could be seen, except such as was due to the colour of the food in the digestive tract. This was also true of earlier stages.	The larva on etiolin remained as white as before. Of the next in size 3 were alive, 1 of which had grown very much, and seemed to be near the end of the 3rd stage. It was very white and maggot-like. The smallest was placed on etiolin. Of the 5 remaining larvæ 2 were alive. 1 was very small, and apparently in the 1st stage, the other probably at end of 2nd stage. Both were placed on etiolin.	Carefully compared. 23 alive in 4 pots. 20 in last stage, and all various shades of brown except 2, which were slightly greenish and distinctly greenish respectively, the latter having only just changed skin. 1 was in 4th stage; 2 were changing last skin (1 green and 1 light brown).
Nov. 9		Of the only 2 larvæ now eating the white	The 3 last mentioned larvæ and the

Dates.	(1) Etiolated leaves.	(2) White mid-ribs.	(3) Green leaves.
		mid-ribs the larger one had grown considerably. The 4 on etiolin were still alive, and seemed to have become yellower, but not more so than was to be expected from the food in the digestive tract.	distinctly greenish one in last stage were kept together and compared at this date. 1 was dead; 1 was small in last stage (dark brown); 2 were large in last stage (1 light brown and 1 somewhat greenish-brown).
Nov. 16		Of the 4 on etiolin 2 were dead (including the larva first placed on it), the others still faintly yellowish.	
Nov. 20		The largest larva was now 21·5 mm. long when extended at rest; the other was dead. Only 1 larva alive on etiolin, and that died Nov. 21.	
Nov. 28		The remaining larva had grown greatly, and was advanced in the 4th stage. A great development of superficial pigment had appeared suddenly between this date and Nov. 20, especially marked upon the brown head, prothoracic plate, and supra-anal plate, and in the dark subdorsal semilunar marks; minute black points were also abundantly scattered over the whitish general surface. The white sub-	

Dates.	(1) Etiolated leaves.	(2) White mid-ribs.	(3) Green leaves.
		dorsal line was opaque, and evidently followed from some structural cause (probably pigmentary) distinct from that to which the pale whitish general surface was due. This was perhaps the case with the white spiracular line also. When at rest the length varied from 20·0 to 22·0 mm. according as the larva was moderately contracted or moderately extended. On December 2 the larva was painted (in the 4th stage) in two attitudes (see Pl. 4, fig. 1).	
Dec. 16		The larva was resting before changing the last skin; it was 29·0 mm. long when extended at rest.	
Dec. 18		The last skin had now been shed, and the larva was *much* darker, although the ground colour seen between the dark pigment spots was as pale as before. Hence the effect was greyish. On the evening of the 17th, before ecdysis, the increase of superficial pigment was observed, especially in the dorsal, subdorsal, and supraspiracular regions.	
Dec. 29		The larva was painted when much grown in last stage (Pl. 4, figs. 2 and 3).	

Dates.	(1) Etiolated leaves.	(2) White mid-ribs.	(3) Green leaves.
Jan. 1, 1893		At this date the larva was offered etiolated leaves, but did not appear to eat at all, and seemed to be hybernating. The appearance did not alter. On Jan. 14th it was killed accidentally.	

Before discussing the conclusions, it will be best to consider the possible effect of certain conditions incidental to the experiments.

Darkness.—The almost continuous darkness probably affected the colours of the larvæ in (1) and (3), as they became mature. Tho adult larvæ of *T. pronuba* are sometimes bright green; and some of the larvæ, hatched from the batch of eggs which supplied these experiments, reared by Miss L. J. Gould in the light and with green surroundings, remained a distinct, although dark, green until maturity, quite unlike any of those referred to above.

Although it is thus probable that the larvæ are sensitive, like so many others, to the colour and degree of illumination of their surroundings, the results of these experiments are not affected in any essential respect; for there was abundant opportunity for comparison *before* the changes referred to had taken place (*e.g.*, October 10), and when the majority of the larvæ in (1) and (3) were green (see Plate 3, fig. 1). Furthermore it is also evident that the comparison was equally valid *after* the change had taken place, inasmuch as the brown ground colour, no less than the green, is shown to be due to a modified plant pigment.

Nutritive Value of Pigmentless Food.—The extremely slow growth of the larvæ fed upon the white mid-ribs, and the death of all except one of them in an early stage, may be looked upon as an argument that they were in a pathological condition, one result being the inability to form a certain kind of pigment. Such an interpretation would, of course, upset the conclusions I have arrived at.

On the other hand, it may be urged that the single larva in (2) which survived until it was advanced in the last stage was certainly not pathological, and yet was unable to form the pigments in question. Although it grew very slowly in early youth, it began to be conspicuous by its size on November 2, and from this date it grew rapidly and fed largely (see Plate 4, figs. 1 and 2); judged by all standards, it was perfectly healthy. Furthermore, everyone who breeds larvæ knows that they are subject to diseases of various kinds, and yet, so far as I am aware, the complete inability to form certain classes of pigment has not been recognised as a symptom. Moreover, the larvæ fed on the thick succulent etiolated leaves (1) grew far more rapidly then those fed on green leaves (3). This species hybernates in the larval state, and, as is usually the case in such species, the rate of growth is extremely irregular. Many of the larvæ reared by Miss Gould, and single larvæ fed upon green leaves by me, lagged far behind the others and yet remained healthy.

I believe that the retarding effect of the mid-ribs was not due to the absence of plant pigments, but to the rapid drying and oxidation of the cut surfaces (left by the removal of the rest of the leaf) and the inability of the young larvæ to get sufficient food from other parts,

where the tough cuticle could not be easily penetrated by their small weak mandibles. The larger larvæ do not experience the same difficulty.

It will be well, however, to repeat the experiment with other larvæ, some of which may be expected to have greater powers of endurance. I would suggest *Mamestra brassicæ* and *Phlogophora meticulosa* as suitable for the purpose. Freshly cut mid-ribs might be offered every day or perhaps twice a day.

Conclusions from the Experiments.—Assuming that the results obtained in Experiment (2) are not pathological, and I believe that this assumption is justified, it follows that etiolin (1), no less than chlorophyll (3), can be transformed into a larval colouring matter, which may be either green or brown, and is so disposed as to form a ground colour.

The fact that *brown* pigments may be thus formed is new. In my previous paper ('Roy. Soc. Proc.,' 1885, pp. 269 *et seq.*) I gave reasons for the conclusion that the green pigments are derived from plants, but argued that brown pigments are proper to the larva. This still remains true in many cases. Thus the green larvæ of *Amphidasis betularia*, investigated in 1892, are coloured by derived pigments contained in the superficial fat, while the brown larvæ are coloured by true pigment contained in the epidermic cells ('Trans. Ent. Soc. Lond.,' 1892, pp. 357—359), so that the green fat which lies beneath is concealed. The intensely opaque and dark larvæ of many other Geometræ are probably similarly coloured by true pigments in the cuticle or epidermis. But the brown ground colour of many Noctua larvæ will probably be found to be due, like that of *T. pronuba*, to modified plant pigments.

A comparison of the larvæ fed on pigmentless food (Plate 3, fig. 2, Plate 4, figs. 1—3) with those fed upon etiolated leaves (Plate 3, fig. 1) and the similar larvæ fed upon green leaves, proves that both green and brown ground colours are modified plant pigments. When the larvæ fed on etiolin were being compared on October 10, one of them became irritated and expelled a drop of fluid from its mouth. This fluid was of a faintly *bluish-green* colour. This observation suggests that the change of etiolin into a soluble green pigment takes place in the digestive tract. Chlorophyll similarly becomes soluble and forms a green solution (turning brown on exposure) in the digestive tract of larvæ. It is possible that the brown ground colour of the larvæ is also a result of oxidation: at any rate, it is a change in the direction of greater stability; for I have shown that the colours of certain brown larvæ, evidently coloured like those of *T. pronuba*, are far more persistent after preservation than those of the green varieties of the same species ('Roy. Soc. Proc.,' 1885, pp. 275, 276).

Although the brown ground colour, probably situated in this

species in the epidermic cells, is thus derived, there is an abundant deposit of true pigment in the form of spots and patches in the superficial cuticle. This was as distinct in the larvæ of (2) as in those fed upon etiolin or chlorophyll; but, the ground colour of the former being white instead of green or brown, it produced a greyish effect (Plate 4, figs. 1—3). The opaque, white stripes in the subdorsal and spiracular regions are also probably due to true pigment situated in this case in the epidermic cells, and are equally conspicuous in the larvæ fed on pigmentless food (Plate 4, fig. 2).

In certain parts of the body the cuticle is of relatively greater thickness—the head, prothoracic dorsal plate, supra-anal plate, true legs, and parts of the claspers. In these situations, therefore, the combination of a deeply-placed ground colour composed of derived pigments with a superficially placed true pigment would not necessarily produce the same effect as in the other parts of the body where the cuticle is much thinner; for the derived pigments would tend to be hidden. In these parts, therefore, *both ground colour and markings are cuticular, while both are composed of true pigment* of such a tint as to harmonise with the effect produced by the combination of two distinct elements in other parts of the body. Hence these parts remained normal in the larvæ of Experiment (2), resembling the brown larvæ of the other experiments, and serving to show what the colour of the rest of the body would have been if the plant pigments had been present in the food (Plate 4, fig. 3).*

Some indication was afforded in the course of these experiments that the power of converting the plant-pigments into metachlorophyll may be lost in larvæ which have been fed from the egg for a considerable time upon pigmentless food. Thus the larvæ of Experiment (2) remained pale when fed upon leaves which caused those of Experiment (1) to become brown or green. At the same time it must be remembered that these particular larvæ were certainly unhealthy, and died soon after the change of food. I hope to repeat this experiment upon healthy larvæ. I have already shown that many larvæ which are normally found upon a variety of food plants will starve rather than eat certain of them when they have been fed upon the others from the egg ('Ent. Soc. Lond. Trans.,' 1887, pp. 312—314). It is possible that a somewhat analogous "gastric education" may take place as regards the digestive action upon plant pigments. But confirmatory experiments, specially directed to test the conclusion, are much wanted.

* [This argument appears to be valid in the case of the older larvæ of this species and probably many others. There are, however, many instances in which the derived pigments are distinctly visible through an extremely thick cuticle (*e.g.*, in the head of larvæ of the genus *Smerinthus*). The distribution of the derived pigments has not been investigated in this case.—October 15, 1893.]

It is of great interest that the etiolin should be as effective as chlorophyll in the production of larval colours. It is, however, probable that the difference between etiolin and chlorophyll is, chemically, extremely small, while both appear to undergo similar changes in the larval digestive tract, yielding a substance which becomes dark coloured on exposure to air, probably by oxidation. Thus of the two heaps of fæces represented in Plate 3, fig. 1, that to the left had been exposed to the air for some hours, and was dark brown, while that to the right was fresh and of a pale-yellow tint. A cut midrib darkens on exposure quite independently of the plant pigments as may be seen in the same figure; but the tint is different, and the depth of shade far less than in the fæces containing abundant etiolin. The fæces of the larvæ fed on pigmentless food similarly darkened far less rapidly and to a much less extent than those of the others.

Although the results of these experiments are, I believe, completely successful in establishing the conclusion they were intended to test, it must be admitted that they point to the beginning of an investigation rather than its end. We now know that certain larval colours are dependent on the existence of modified plant pigments, and this naturally leads to an enquiry into the nature and causes of the processes by which chlorophyll and etiolin are converted in the animal body into a comparatively stable green or brown substance far removed from its original position in the digestive tract, and situated so as to form an important element in the effective colouring of the individual.

Description of Plates 3 and 4.

Plate 3.

Fig. 1.—A group of five larvæ of *Tryphæna pronuba* in the 4th stage, natural size. These larvæ had been fed entirely upon the etiolated leaves of cabbage. They had hatched September 7 and 8 (1893) and were painted October 10. Nearly all the shades of colour observed in the larvæ at this stage are represented in the figure, four being various shades of green, and one brown. It is clear from the figure that the larvæ can form a deep green colouring matter from etiolated leaves. There was, in fact, no difference in this respect between them and larvæ fed on green leaves.

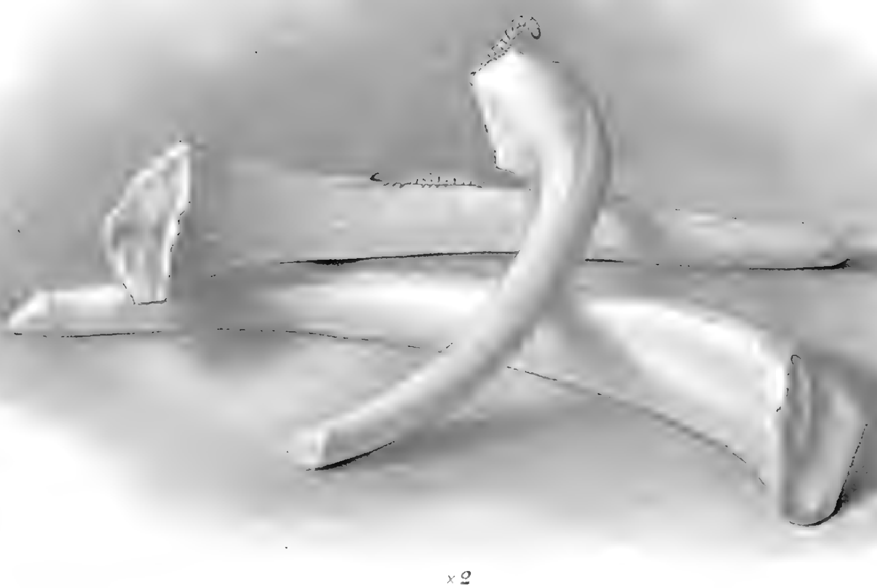
The marked contrast in colour between the green larvæ and the leaf is some indication of the change which the etiolin has undergone in the larval body. The dark marks along the sides are due to superficially placed true pigment, which is formed independently of any coloured substance in the food plant.

Two heaps of fæces are represented in the figure: that to the right

1.

Natural Size

2.

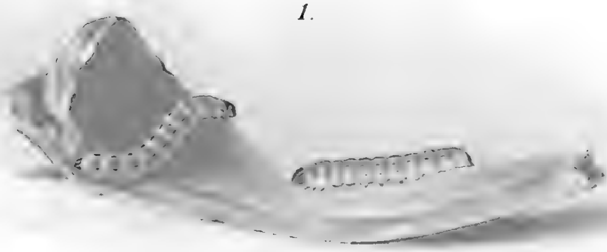


× 2

P. J. Bayzand pinx.

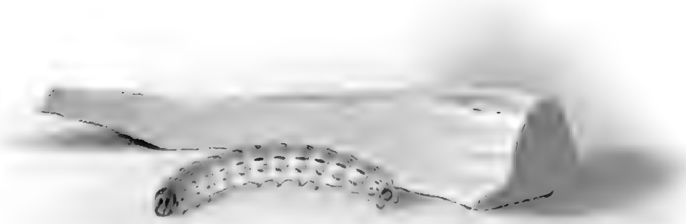
Lith. Werner & Winter, Frankfort º/M.

1.



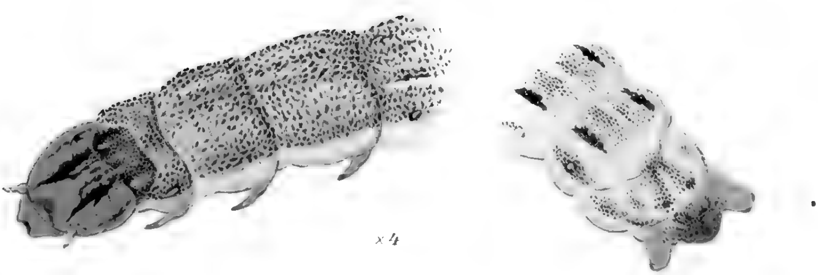
Natural Size

2.



Natural Size

3.



× 4

fresh, and pale yellow in colour; that to the left exposed to the air for some hours, and dark brown.

Fig. 2.—A group of three larvæ, of the same species, in the 2nd stage, twice the natural size. These larvæ had been fed entirely upon the white mid-ribs of cabbage leaves. They had hatched September 8, and were painted October 11. While the larvæ represented in fig. 1 were rather larger than those fed on green leaves, these are *much* smaller. The colour is white, and maggot-like, the faint greyish appearance being due to superficial true pigment. Except upon the head, there is not a trace of either the green or the brown ground colour invariably found in the larvæ of this species under normal conditions. Furthermore, these larvæ are uniform in appearance, although the normal larvæ are extremely variable.

A comparison between figs. 1 and 2 proves that the brown or green ground colour of the species is due to some modification of etiolin (or chlorophyll in the case of normal larvæ), unless indeed the results are to be explained as pathological—an interpretation opposed to the facts represented in the figures on Plate 4.

Plate 4.

Fig. 1.—Out of about fifty larvæ which hatched September 8, and were fed on white mid-ribs, a single one began to be conspicuous by its size on November 2, and from this time it grew rapidly, and was evidently quite healthy, although all the others were dead by November 21. On December 2 it was painted (natural size) in two positions, being in the 4th stage. The ground colour remained white or cream-coloured; the grey effect being caused by superficial true pigment, which is seen to be especially marked upon the brown head, claspers, thoracic legs, prothoracic, and supra-anal plates, and upon the dark subdorsal semilunar marks.

Fig. 2.—The last skin was changed by December 18, and, on the 29th, the larva was again painted of the natural size, when advanced in the last stage. The ground colour remained the same, but an increase in the true pigment caused the larva to become a darker shade of grey. A row of supra-spiracular dark markings also made their appearance. The white subdorsal line and, perhaps, the spiracular line were evidently due to some cause of colour (probably pigmentary) distinct from that on which the pale ground colour of the general body surface depended.

Fig. 3.—At the same date the head and anterior segments were painted, × 4 diameters. In those parts where the cuticle is thickened, the head, prothoracic plate, and thoracic legs, a brown ground colour (as well as the black spots and patches) is developed from true pigment in the cuticle itself. Hence these parts remain normal when

the larvæ are fed upon leaves without chlorophyll or etiolin. But over the general surface of the body the cuticle is very thin, and only contains the black spots and patches of true pigment, while the brown or green ground colour, derived from plant pigments, is subcuticular in position. Hence in a larva fed on pigmentless parts of leaves, represented in fig. 3, this latter ground colour is replaced by a creamy tint which is due to the uncoloured tissues of the body, especially the fat, and to the contents of the digestive tract. This creamy ground colour, combined with the spots of true pigment in the cuticle, produces the general greyish appearance of these larvæ.

The posterior segments of the larva, painted at the same date, × 4 diameters, are also represented in the figure, indicating that the thickened cuticle of the supra-anal plate (which possessed a sharper outline than that represented in the figure) contains both brown ground colour and black spots of true pigment, while the general surface presents the combination of a white ground colour and dark spots, conferring a grey appearance.

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XXIV. *On the sexes of larvæ emerging from the successively laid eggs of* Smerinthus populi. By Edward B. Poulton, M.A., F.R.S., F.L.S., &c., Hope Professor of Zoology in the University of Oxford.

[Read November 8th, 1893.]

My friend and former pupil, Mr. R. C. L. Perkins, once told me that he had sometimes noticed that a pair of *Sphinx* larvæ found in the same stage of growth, in close proximity upon the same tree, and presumably hatched from a pair of eggs laid by the same parent, produce moths of different sexes. He inferred that this arrangement facilitated pairing, and he was led to wonder whether there is a regular alternation of sex in the successive offspring.

On the other hand, it appeared quite possible that the cases which he had observed were exceptional, and that the succession is irregular, or that it is such as to facilitate intercrossing rather than frequent pairing between closely related individuals. This latter view is suggested as a probable one by the numerous adaptations by which wide intercrossing is favoured in other departments of organic nature, and by the following direct evidence. Mr. W. Hatchett Jackson and Mr. O. H. Latter have observed that the pupæ obtained from different batches of larvæ of *Vanessa io* "were principally, but not entirely, of one or of the other sex." * It is generally admitted that the separate colonies of *Vanessa* larvæ are, at any rate as a rule, hatched from different batches of eggs. Such an observation, if confirmed, is to be interpreted by one of two suppositions. We must either suppose that the whole mass of eggs of each female *Vanessa* produces a great preponderance of one and the same sex (males in some individuals and females in others), or that different batches of eggs laid

* Trans. Linn. Soc. Lond., vol. v., 1890, p. 156.

by the same individual produce now a preponderance of one sex, and now of another. Either of these alternatives would appear strongly to favour intercrossing. The following observations, so far as they go, tend to support the latter alternative.

A pair of *Smerinthus populi* were found *in coitu* in an Oxford garden, between 10 and 11 a.m., on May 25th, 1893. They were carefully removed, and remained together until 8.40 p.m. The attempt was made to observe the order in which the eggs were laid, and to rear the larvæ separately, the sexes being determined in the pupal state. The results are most concisely shown in a tabular statement.

Date.	Number and order of eggs laid.	Sexes produced. M = male; F = female.	Observations.
May 25.	44 eggs laid, order unnoted.	15 M 28 F	1 missing (unknown whether the egg hatched). 1 male and 1 female moth emerged in the hot summer of 1893. 1 male pupa was deformed and dead.
May 26.	47 eggs laid.	—	All these eggs, the order of which had been carefully noted, hatched during my absence from home, and the larvæ were lost.
May 27.	34 eggs laid. The order of the first 22 unnoted.	9 M 8 F	4 missing; 1 larva died. 1 female moth emerged 1893. 1 male pupa was deformed and dead, and another rather deformed.
	23	—	Larva died small (probably 3rd stage).
	24	.. .. M	Pupa rather deformed.
	25	.. .. F	
	26	.. .. M	
	27	.. .. M	
	28	.. .. M	
	29	.. .. M	
	30	.. .. M	
	31	.. .. F	
	32	.. .. F	
	33	.. .. M	
	34	.. .. M	Moth emerged 1893.
		Total 17 M, 11 F	

Date.	Number and order of eggs laid.	Sexes produced. M = male; F = female.	Observations.
May 28.	28 eggs laid, order shown below.		
	1	F	Moth emerged 1893.
	2	F	
	3	F	
	4	..	Larva died in 3rd or 4th stage, owing to accident to branch of food-plant.
	5	M	
	6	F	
	7	F	
	8	..	Larva died in 3rd or 4th stage.
	9	M	
	10	F	
	11	M	
	12	M	
	13	M	
	14	M	
	15	F	
	16	M	
	17	M	
	18	F	
	19	M	
	20	M	
	21	F	
	22	M	
	23	F	
	24	F	
	25	F	
	26	F	
	27	M	
	28	M	
		Total 13 M, 13 F	
May 29.	8 eggs laid, order unnoted.	4 M 2 F	1 missing; 1 larva died. 1 male moth emerged 1893. 1 male pupa dead and deformed, and 1 very small and rather deformed.
May 30.	14 eggs laid. order unnoted.	7 M 4 F	3 larvæ died.
May 31.	7 eggs laid, order unnoted.	1 M 6 F	
June 1.	3 eggs laid, order unnoted.	1 M 1 F	1 egg did not hatch.

Date.	Number and order of eggs laid.	Sexes produced. M = male; F = female.	Observations.
June 2.	7 eggs laid, order shown below.		
	1	F	
	2	M	
	3	F	
	4	F	
	5	..	Larva hatched, but died very small.
	6	..	Did not hatch. Probably no development took place; egg blackened.
	7	..	Ditto. ditto.
		Total 1 M, 3 F	
June 3.	1 egg laid.	——	Larva did not hatch, but was apparently fully formed in the egg.

The total number of eggs laid on each successive day forms an interesting curve rising to a maximum on the second day and declining very rapidly on the fifth.

The most striking result shown in these tables is the remarkable change in the proportion of the sexes on different days. Thus on May 25th there were nearly twice as many females as males, on May 27th over 50 per cent. more males, while on May 28th the numbers were equal. It is possible that this change in proportion may follow some biological law, especially when considered in connection with Mr. Jackson's and Mr. Latter's above-mentioned observations. It is at any rate enough to suggest further observation. At present, however, as I learn from Mr. Francis Galton, to whom I have submitted the figures, the numbers are not large enough to warrant any such conclusion.

With regard to the succession of the sexes in a series of individuals (May 27th, 28th, and June 2nd), the arrangement does not appear to differ from that of black and white balls drawn successively out of a bag containing equal numbers of each. But here, too, wider observations are required. The arrangement in little groups of the same sex *may* possibly be adapted to favour cross-fertilisation. But even in drawing pairs of

black and white balls, two of the same colour will be drawn together twice as frequently as those of different colours. In future observations of a sluggish species like *Smerinthus populi*, it would be desirable to track the moth as it lays little groups of eggs on different leaves, and to rear such groups separately. We must not altogether put aside the remote possibility that the parent may possess some power of controlling the sex of her offspring.

Six moths emerged in the hot summer of 1893 ; three of these were males and three females. The eggs from which these individuals were hatched were scattered through the successional series, and were not peculiar to any part of it, and the same appears to be true of the deaths of larvæ and deformity of pupæ.

Failures to hatch, however, are confined to the end of the series, unless some of the "missing" larvæ are to be explained in this way. This tendency is especially clearly seen on the last two days, and yet the very last egg laid contained a well-formed larva which was unable to hatch.

Even the small number of larval deaths which took place are chiefly to be accounted for by the conditions of the experiment. Thus, considering only the eggs laid during May (and omitting the later eggs because of the frequent failure to hatch), we find out of 40 larvæ reared in separate sleeves (23 to 34 on May 27th, and the 28 on May 28th) only two deaths occurred, not including the manifestly accidental death of the fourth larva on May 28th. On the other hand, out of 95 larvæ reared in groups of from 3 to 8 (usually 7) in number, 11 larvæ died or were missing. From this it may be inferred that larvæ are in some way injured by being reared in groups with a much greater relative proximity than in nature. I have also found this to be true of *S. ocellatus ;* for, when groups of more than 10 or 12 small larvæ were enclosed in sleeves of moderate size, it was always found that the numbers became reduced to a maximum of about a dozen, and often much lower ; whereas groups of smaller numbers were frequently maintained without any deaths.

The list as a whole strongly impresses upon us the comparative rarity of death from internal causes (including disease), and the overwhelming importance of

the struggle with highly organised enemies in determining the vast amount of destruction which occurs among these animals in the natural state.

The unfortunate loss of the 47 larvæ of May 26th served to show that the period of development within the egg is extremely uniform. The eggs laid on May 25th had been properly enclosed, and I thought I was safe in leaving the others for a day. On my return every one of the eggs laid on the 26th had hatched, and the larvæ had escaped; while not a single larva had emerged from any egg laid at a later date.

Six of the male pupæ were deformed, but not one of the females.

The total number of eggs laid was 193, and subsequent dissection revealed a single egg in the body of the parent moth. From these eggs 68 female and 59 male pupæ were obtained.

The results afford no support to the opinion that the sex of insects can be determined by external conditions during larval life. With conditions of very complete uniformity, the proportions of the sexes—68 females to 59 males—appear to be normal. It may be admitted that the larger female larvæ require more food, chiefly to prepare for the amount of material to be stored up in the ova. It would not therefore be at all surprising if the female larvæ were starved before the males when a minimum of food was supplied. The consequent emergence of a number of males would in no way support the view that a scanty diet "determines" this sex. It is probable that some writers on this subject have mistaken *favouring* for *determining* conditions.

There was no tendency towards the predominance of males in the last-laid eggs, and therefore no indication that this sex may be determined by exhaustion (in itself most improbable) of the spermatozoa.

XVI. *Mr. Merrifield's Experiments in Temperature-Variation as bearing on Theories of Heredity.* By Frederick A. Dixey, M.A., M.D., F.E.S., Fellow of Wadham College, Oxford.

[Read March 14th, 1894.]

The results of Mr. Merrifield's experiments on the variations produced in butterflies by the exposure of the pupa to different conditions of temperature, are in themselves of great interest. But the interest becomes enhanced when it is recognized that many of the new features which make their appearance under these conditions are identical with those occurring normally in other species more or less closely allied to the subjects of experiment; that in not a few instances the disturbance of natural temperature-conditions appears to have caused reversion to an earlier stage in the phylogenetic history of the species; and further, that the ancestral features thus revived seem to vary with the nature of the disturbance.

Examples of these phenomena, from a previous series of experiments, were given in Trans. Ent. Soc. Lond. 1893, p. 55, and were commented on by me (*Ibid.* p. 69). The latest results obtained by Mr. Merrifield, besides confirming many of the former, furnish further instances of the same nature, as follows:—

I. Vanessa atalanta.

A. *Warmed.*

(1) The occurrence of red scales in the dark ground-colour between the middle of the scarlet band and the large white costal spot c. This is an approach to the condition in *V. huntera* and *V. myrinna,* and more remotely to that in *Grapta* and *Argynnis.* A corresponding feature is seen in *V. io,* which in this respect is more ancestral than *V. atalanta.*

(2) The tendency towards the formation of a scattered ring of red scales round the spots β and γ of Series D.

This again recalls a common condition in *V. myrinna* and *V. huntera.*

(3) The appearance of a new red spot on the under-side of the forewing, just below the stem of the median nervure before bifurcation. This represents a pale patch of various shades in *V. callirrhoe, V. myrinna, V. huntera, V. cardui,* etc.

(4) The appearance of another red spot on the under-side of the forewing, just below the first median nervule. This represents a patch visible on both surfaces of *V. callirrhoe,* and fully developed in all the species nearly allied to *V. cardui.*

(5) The tendency towards resolution of the inner margin of the red band, as in *V. callirrhoe.*

(6) The suffusion of the dark ground colour with golden brown, also as in *V. callirrhoe.*

Of these, Nos. (1) (2) and (3) are points now observed for the first time; while (4) (5) and (6) are confirmations of previous results. (See a former paper by the author in Trans. Ent. Soc. Lond. 1893, p. 70.)

B. *Cooled.*

(1) Much substitution of lavender or metallic blue-green scales for black. This points to the ancestral condition seen in the females and parts of the males in many species of *Argynnis, e.g., A. paphia,* var. *valesina, A. sagana* ♀, *A. niphe* ♂ and ♀, and *A. diana* ♀.

(2) The presence of minute patches of bluish scales near the margin of the dark ground-colour in the hind-wing, indicating the blue centres of the almost completely merged Series III.—an ancient feature of *Vanessa* and *Grapta.*

(3) The marked increase of marginal blue, especially about the anal angle of the hindwing. This appears to represent the condition seen in *Argynnis niphe,* and ultimately to point back to the primitive Argynnid colouring of *A. valesina* and *A. diana* ♀.

These are all confirmations of former results.

II. Vanessa io.

In this species, warming tends to revive, in the fore-wing, a series of dark spots (II), occurring normally in

Araschnia levana. Cooling tends in the first place to separate certain constituents of the ocellus, and when carried to a high extent has the remarkable effect of causing an unmistakable resolution of the ocellus in the forewing, the appearance finally produced being that of the ordinary *Vanessa* character in a comparatively unmodified form. It is interesting to see how completely these cooled specimens bear out the views which I ventured to express, some years ago, on the origin and constitution of this ocellus (Trans. Ent. Soc. Lond., 1890, pp. 99, 100, pl. i., fig. 12). The ocellus of the hindwing is also affected in the same direction.

III. Vanessa polychloros.

Cooling tends to produce several features which appear to be ancestral. The chief of these are (1) the pupilling with black of the spots of Series D in the forewing; (2) the occasional indication of Series III. in the hindwing; and (3) the tendency towards the formation of a new dark spot between II.8 and III.8. These points approximate towards the condition in *Grapta.*

IV. Grapta c-album.

In both broods cooling tends to induce or increase a darkness of ground-colour; this being undoubtedly an ancestral character.*

In all cases of this kind the obvious question occurs—are we to consider these phenomena as true instances of reversion, or is it merely that like causes have produced *de novo* a like effect in descendant and ancestor? The latter explanation may account for some of the facts, but, I think, not for all. It may perhaps give the reason for a general diffusion of bluish scales, or for a change of the ground-colour from black to brown, but it is scarcely adequate to explain the special formation of a definite pattern, as of Series III. with its blue centres in *V. atalanta*, or the reduction of the ocellus in *V. io* to the primitive *Vanessa* condition. Without raising the vexed question of sexual selection, we may yet affirm that

* The observations on the three last species are new ; those on *V. atalanta*, as has been seen, are partly new and partly old. On the whole subject of the ancestral markings in *Argynnis* and *Vanessa*, see the author's paper in Trans. Ent. Soc. Lond., 1890.

among the features induced or revived by altered temperature-conditions, there is at least a residuum which must have owed its first origin to causes other than the direct action of temperature on the organism. Nor, again, are these to be considered as cases of "arrested development"; for the stages reproduced are stages in the phylogeny of the species, not in the ontogeny of the individual.

If, then, these revived features are really ancestral, how is their revival to be accounted for? The whole subject of reversion abounds with difficulty. An explanation commonly offered is that the characters last developed in the history of a species, or of an individual, are less stable than those that have a longer history behind them, and that have become firmly established under the operation of a long-continued process of heredity. Any disturbance—such as an exceptional condition of temperature—of the normal course of growth, may therefore be expected to act in the first place on the newer and less stable features, interfering with their usual line of development, and shaking back the species as it were to an earlier and more firmly-founded stage of its development—just as in an earthquake the freshly-built wing of a house, where the mortar was not yet dry, might fall and leave the older portions standing. Such an explanation, however, is in itself at best but partial, for it gives no real reason why the newer features should be less stable than the old; and indeed it comes to little more than restating the difficulty in another form.

The two attempts to find a more definite explanation of reversion which may be said at present to hold the field, are those which pass respectively under the names of Darwin and Weismann. If the Darwinian assumption of centripetal "gemmules" be granted, the commonest case of reversion, that namely which results from hybridization, especially between recently-established species, is capable of explanation under the hypothesis of pangenesis. But it may be questioned whether pangenesis as stated by Darwin is capable of accounting for such cases as the present, inasmuch as in them the condition of full maturity is almost reached before the introduction of the modifying disturbance. Although the ovum from which the individual has originated may under the Darwinian hypothesis have contained numerous gemmules of an

ancestral type, which though usually dormant might under certain circumstances become active in the ontogenetic process, it would yet seem a legitimate conclusion from the hypothesis, that the introduction of any cause analogous to hybridization in its action on the developing organism must belong to a far earlier stage in the ontogeny than the beginning of the pupal condition; it must belong, in fact, to the stage of fertilization of the ovum. There are, however, a few facts on record, such as the assumption of ancestral characters by an old hen (Darwin, "Animals and Plants under Domestication," 1868, vol. ii., p. 54), and the appearance of an earlier vertebrate condition in limbs of Amphibia reproduced after amputation (*Ibid.*, ii., p. 15), which seem in some respects analogous to the present instances, as being apparently cases in which a disturbance of normal conditions at a comparatively late ontogenetic stage has in some way led to reversion in the course of the individual growth. These cases are regarded by Darwin as not incompatible with pangenesis, though not fully explained by it.

If, on the other hand, we postulate with Weismann the existence of "ids" and "determinants," endowed with the nature and properties that he supposes, the instances that we are considering become more explicable. For according to this theory every feature in the structure of the individual organism is the result of a "struggle of the ids" in ontogeny, the final character of each histological unit being fixed at the moment of the liberation of its proper determinants by the disintegration of the "ids." The competition between the carriers of heredity, many of which must under the theory be ancestral in character, so far from being confined to the ovum, is being waged throughout the entire ontogeny, and is renewed at every successive stage of development. This being the case, it is to be expected that any external influence, such as temperature, on coming into force at any given stage, should be able to exert an effect upon the struggle proceeding at that particular time between determinants which are just beginning to play their parts in the ontogeny, and should in consequence be able to modify *pro tanto* the resulting adult organism. It would be, moreover, natural to expect the different determinants to be affected by different temperatures, nor would it be surprising to find that temperature-conditions, which are

ex hypothesi diverse from those normal to the species, should favour one or other set of ancestral determinants at the expense of those more proper to the species. This would explain why the effect of heat differs from that of cold, though both lead to reversion.

There is, however, one fact which shows that the above explanation is not entirely adequate—the fact, namely, of the hereditary transmissibility of certain temperature modifications, as determined in the case of *Polyommatus phlœas* by Weismann himself ("The Germ-Plasm," 1893, p. 399). This phenomenon admits of a ready explanation under the theory of pangenesis; the point that pangenesis fails to explain is the reversionary character of the original change, unless, indeed, we suppose a "struggle of gemmules," analogous to the "struggle of determinants," and continued, like the latter, throughout the ontogeny; in which struggle certain conditions favour the ancestral rather than the modern gemmules. But just as the theory of pangenesis seems to require some such addition as that suggested, so also, under the rival hypothesis, it seems necessary to supplement the explanation above given with another supposition already propounded by Weismann, namely, that the temperature-conditions are capable, in some cases, of actually altering the constitution of unexhausted determinants wherever they occur, even in the germ plasm of the ovum itself.

I am myself inclined to think that, granting Weismann's general theory of heredity, the more special cases of reversion are to be chiefly explained, as above, by the critical influence of the temperature-conditions on the struggle of the determinants, rather than by an intrinsic effect on the determinants themselves. The latter may account for such cases as a general lightening or darkening of the ground-colour, as in Weismann's *P. phlœas*, which strictly speaking are not really but only accidentally reversionary; it will not, however, account in my opinion for the special ancestral marks shown by Mr. Merrifield's *V. atalanta* and *V. io*.

The point is capable of verification. If it be true that there is a selective influence which is exerted upon the actual struggle of the determinants, that influence would find a different expression in the adult according to the particular stage in the ontogeny at which the influence was applied, as it would affect those determinants only

between which at that time the struggle was being waged.* If, on the other hand, there is no such influence, but the effect is entirely a direct one and modifies the individual determinant, then all the as yet unexhausted determinants that are capable of reacting to this particular disturbance would be affected in some degree; though no doubt, as Weismann supposes, to a greater extent if they had reached the point of disintegration than otherwise.

Again, it seems to me to be of great importance to ascertain if possible which of these modifications are transmissible to descendants. If all the modifications, including those which I have supposed to be produced in the first way, can be shown to be hereditarily transmissible, this would amount to a demonstration that the second explanation is adequate; and the first may then be abandoned as unnecessary. Should only some be inheritable, the presumption would be in favour of the co-existence of both modes of action; moreover, the greater the number of non-transmissible variations that can be produced, the more will the case be strengthened against pangenesis, and in favour of the "centrifugal" theory.

I am anxious to see, if possible, the results of breeding experiments on specimens like these for yet another reason. It seems to me that by comparative experiments, with and without artificial selection, on such variations as may be transmissible, a measure might be obtained of the relative importance of selection and the mere action of external influences in the transformation of a species. I think, too, that no better group for such experiments as these of Mr. Merrifield's could be selected than the Vanessas. For, in the first place, it is only among poikilothermic animals that the *direct* effects of temperature can be fully studied; then among these the Lepidoptera are pre-eminent for the extremely delicate register of variation afforded by their wings; and, lastly,

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* The fact that in *V. polychloros* forcing invariably tends to produce a certain effect, whether preceded by warming or cooling; while refrigeration brings about another definite effect, whether followed or not by forcing, seems so far favourable to this hypothesis. See above, p. 432.

among the Lepidoptera the Vanessas belong to an assemblage the phylogeny of which may claim to be at any rate partially known.* It is hardly necessary to point out how much service may be rendered to researches of this kind by the careful working out of the true internal affinities of Lepidopterous groups. In proportion as their phylogeny is placed on a secure basis, we shall be able to pronounce with confidence on the real character, whether reversionary or not, of these remarkable variations; and shall accordingly be able to estimate at its proper value the evidence they bring towards the solution of the great problem of Heredity.

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* See the author's paper already referred to, in Trans. Ent. Soc. Lond., 1890, p. 89.

EXTRACTED FROM THE PROCEEDINGS

OF THE

ENTOMOLOGICAL SOCIETY OF LONDON

Of 20th March, 1895.

Mr. F. Merrifield exhibited some *Limenitis sibylla*, the pupæ of which had been subjected to extreme temperatures. A temperature of 85° to 90° was fatal to most; in those which survived the black ground-colour is pale and freckled, and there is some increase in the reddish scales near the apex of the forewings and the anal angle of the hindwings; and on the underside the orange-brown ground-colour is increased in area and is much lighter and more orange in its colouring. The pupæ endured cold better than heat. Icing from 8 to 40 days, followed by a normal temperature for 12 to 14 days, produced no sensible alteration of markings or colouring, but an exposure to a temperature of about 48° for 22 days and up to 36 days caused a sprinkling of the white band with black scales; the most sensitive part in this respect is in the hindwings, the interspace between the costa and the next nervure; here it is so dense as to turn the white to a dull grey. On the underside this cooling caused a slight increase in the area and intensity of some of the darker parts, but this was counteracted by a tendency to suffusion and spreading of any white parts. He thought that this species would bear a longer exposure to a low temperature than he had ventured on trying. He also showed a long series of *Vanessa C-album*, the larvæ of which had been kindly sent him, in May last, by Mr. Allan Nesbitt of Llandogo, Monmouthshire. Though subjected to more severe cold and for longer periods than those experimented on in 1893, as recorded in the

Transactions for that year, they showed no very considerable increase in the results obtained. Some, however, showed a substantial increase of the area and intensity of the dark parts and a darkening of the light parts, besides the occasional appearance of a few blue or lavender scales in places where, according to Dr. Dixey, they had a special significance. Mr. Merrifield stated that Dr. Standfuss had published some temperature experiments on this species which, as he had found, had shown itself not so sensitive to pupal temperature as some other species of *Vanessa* had proved themselves to be. Unexpectedly he (Mr. Merrifield) had found the species to be distinctly more intolerant of cold and less intolerant of heat than is *L. sibylla*. Experiments on a few pupæ of *Vanessa cardui* in 1894, showed this insect to be extremely sensitive in its colouring and markings to both high and low temperatures; this was quite in accordance with the experience of Dr. Standfuss, who had described the great results obtained by his experiments with this species.

Dr. Dixey said that Mr. Merrifield had kindly given him the opportunity of carefully examining the specimens exhibited that evening. With regard to the specimens of *L. sibylla*, he should prefer to reserve his remarks for another occasion, but in the fine series of *V. C-album* he noticed many individuals as to which he might say at once that they seemed to bear out in a most interesting way the conclusions arrived at from former experiments, conducted both by Mr. Merrifield and by Dr. Standfuss, with other species. They showed evident marks of reversion, and these marks were again of so special a kind as to preclude the supposition that they were the direct result of changes of temperature. The most remarkable of these features, *i.e.*, the well-developed condition of Series III., and the presence of blue points in the dark patches composing it, might be seen in a conspicuous form in the Chinese species *Vanessa* (*Grapta*) *C-aureum*, which insect was for many reasons to be considered as one of the oldest surviving representatives of the Vanessid group. There could, then, be little doubt that in this instance, as in so many others, Mr. Merrifield had succeeded, by the introduction of altered conditions, in producing a reversion to a more ancestral form than that normally assumed by the species. The more these instances ac-

cumulated, the more they seemed to him to strengthen the conclusion that the altered temperature-conditions were capable of acting as a stimulus to which each organism would respond according to its own pre-arranged constitution, and that it was only in comparatively rare cases that the new conditions operated as the *causa efficiens* of the change. (See Weismann's Romanes' Lecture, 1894.) Even in such an instance as that of *P. phlœas*, it was, perhaps, too much to assume that the darkening of the scales was the direct result of a high temperature, for in other cases the same temperature-conditions led to the opposite result. If we pushed the matter further and proceeded to ask what was the nature of the pre-arrangement of material which enabled different species, during growth, to respond in a different manner to the same stimulus, and in many cases to respond by reverting to an earlier phylogenetic stage, we found ourselves at once on very debatable ground. It might, however, safely be borne in mind that under either of the two leading theories of heredity —the centripetal and centrifugal—it was perfectly conceivable that a competition took place during the growth of every organism between various elementary constituents—call them what we please—the greater number of which were destined to take no part in the somatic structure of the adult organism, though they might still be transmitted in a latent condition, through the germinal material, to succeeding generations. To the revival into efficient activity, under exceptional conditions, of some of these usually latent "determinants" or "gemmules," he was inclined to attribute such remarkable instances of atavism as those now exhibited by Mr. Merrifield.

Mr. Barrett said he was interested to find that one of the forced forms of *L. sibylla* was similar to a specimen he had seen which had emerged from the pupa during a thunder-storm.

Mr. F. W. Frohawk, in connection with Mr. Merrifield's paper, exhibited a series of 200 specimens of *V. C-album* bred from one female taken in Herefordshire, in April, 1894. The series consisted of 105 males and 95 females, and included 41 specimens of the light form, and 159 of the dark form.

Professor Meldola, in proposing a vote of thanks to Mr. Merrifield, Dr. Dixey, and Mr. Frohawk, said that he was glad to think that the subject of Seasonal Dimorphism, which had been first investigated systematically by Weismann, was receiving so much attention in this country. He was of opinion that the results hitherto arrived at were quite in harmony with Weismann's theory of reversion to the glacial form and all the evidence recently accumulated by the excellent observations of Mr. Merrifield and others went to confirm this view as opposed to that of the direct action of temperature as a modifying influence.

Mr. Merrifield, Mr. Barrett, and Dr. Dixey took part in the further discussion which ensued.

On the Relation of Mimetic Characters to the Original Form. By F. A. DIXEY, M.A., M.D., Fellow of Wadham College, Oxford.

(Abstract.)

An objection that has been often brought against the theory of mimicry, as enunciated by Bates and accepted by Darwin, is the difficulty of imagining the first stages in the production of a mimetic pattern. Fritz Müller* endeavoured to meet this objection by alleging that mimicry chiefly originated between forms that already bore considerable resemblance to each other. The main instance (that of *Leptalis melia*) on which he relied in order to prove his point was not well chosen, for there is reason to think that he was in error both in considering that this species represented the ancestral form of *Leptalis* and in supposing that it was not protected by mimicry. Nevertheless his contention is sound in so far as it emphasises the fact that the process of mimetic assimilation depends rather on the development of old than on the starting of new features.

An illustration of this principle is afforded by a comparison of the non-mimetic butterflies *Pieris locusta* and *P. thaloe* with the mimetic species of the closely allied genus *Mylothris*, and with *Heliconius numata*, which serves as the model for the latter; all these forms inhabiting the same part of the neotropical region. An almost perfect transition can be traced on the undersides from the non-mimetic species of *Pieris* through *M. lypera* ♂, *M. lorena* ♂, *M. pyrrha* ♂, *M. lorena* ♀, to *M. pyrrha* ♀, this last butterfly being a very close copy of *Heliconius numata*. The whole series shows (1) that a practically perfect mimetic pattern can be evolved by gradual and easy stages without any violence or abruptness of change; (2) that it is not necessary that the forms between which mimicry originates should possess considerable initial resemblance; (3) that so small a beginning as the basal red

* Jenaisch. Zeitschr., vol. x., 1876.

patches on the underside of the hind-wing of many Pierines gives sufficient material for the assimilative process to work upon.

The feebler development of the mimetic pattern in the males of this group calls for some explanation. No doubt the females stand in greater need of protection, but does there exist any active check on the fuller assumption of mimetic patterns by the males? The retention of the original white by the latter sex has been in similar instances attributed to female choice; Mr. Wallace on the other hand thinks it due to the difference of habits in the two sexes, the females alone flying in company with the mimicked *Heliconii*. But this leaves unexplained the presence of a *partial* mimetic pattern in the male. The probability is that although on the wing it may be advantageous rather than otherwise to the male, as Mr. Wallace thinks, to be taken for an ordinary white butterfly, yet when the insect is at rest, and settled with the wings erect, any Heliconine resemblance would be to some extent protective; and the whole aspect of these males, the underside alone of which shows any mimetic features, is the resultant of these two divergent tendencies. The mimetic features of the male cannot be regarded as a mere incidental result of the more complete transformation of the female, because in many species of other groups the female is completely mimetic while the male shows no approach whatever to a mimetic change; moreover there is a species of *Hesperocharis* (*H. hirlanda*) in which not only the male but both sexes show a partial mimetic pattern no further advanced than that of *M. lorena* ♂ or *M. pyrrha* ♂. It is difficult to believe that in this case the pattern is not in some degree protective.

Red basal spots like those of the mimicking Pierines are in some cases found in the mimicked *Heliconii*; this is especially the case in those that form models for the Pierine genera *Euterpe* and *Pereute*. These spots are too widespread in the Pierine subfamily to have arisen from imitation of the *Heliconii*; their presence in the latter is probably due to "reciprocal mimicry" between distasteful forms, as suggested by the author in Trans. Ent. Soc. Lond., 1894, p. 298.

A curious case of a mimetic assemblage is afforded by the Pierines *Euterpe critias* and *E. bellona*, together with their respective models *Papilio zacynthus* and the *Heliconii* of the *thelxiope* group. The *Papilio* and the *Heliconii* have no close resemblance to each other; but appear to be held together, as it were, by the intermediate Pierines. If the *Heliconii* are considered as the models for the whole group, the question arises why *E. critias* should copy a mimic (*P. zacynthus*), and not a very good one, instead of the original distasteful model (*Heliconius*). It is more probable that here also we have an instance of an "inedible association"; this conclusion being strengthened by the fact that a certain amount of "give and take", or "reciprocal mimicry", seems to have occurred not only between the *Heliconii* and the Pierines, but also between the Pierines and the *Papilio*.

The paper was illustrated by coloured drawings of the species referred to.

August, 1894.

[*From the British Association Reports*, 1894.]

III. *On the Relation of Mimetic Patterns to the Original Form.** By Frederick A. Dixey, M.A., M.D., F.E.S., Fellow of Wadham College, Oxford.

[Read Feb. 5th, 1896.]

Plates III., IV., & V.

I. The Gradual Growth of a Mimetic Pattern.

It is now many years ago that Fritz Müller published an answer to those opponents of the theory of mimicry who made much of the difficulty of accounting for the first advances towards the formation of a mimetic pattern.† In the course of this communication he pointed out (as indeed Darwin had done before him) that mimicker and mimicked might, in many instances, be reasonably supposed to have started, not from a position of wide divergence from each other, but rather with the possession of some feature or features, common to them both, which should give material ready to hand for the assimilative process to work upon. The chief instance relied on by Fritz Müller in support of his contention was the well-known mimetic genus of Pierine butterflies known as *Leptalis* or *Dismorphia*.‡ The black and yellow *Leptalis* (*Dismorphia*) *melia*, according to him, was to be regarded as representing the primitive type of coloration of the genus; and although it did not itself mimic any other form, it nevertheless showed independently so much of the characteristic Heliconine colours and arrangement of pattern, that the complete Heliconine aspect presented by many of its near relatives could be derived from it with comparatively slight modification.

* A preliminary abstract of the present paper has appeared in the British Association Reports for 1894.

† "Einige Worte über Leptalis," Jenaisch. Zeitschr., vol. x., 1876, p. 1.

‡ The old genus *Dismorphia* has been divided by Messrs. Godman & Salvin into *Dismorphia*, *Pseudopieris*, *Enantia*, and *Acmepteron*, Biol. Centr.-Amer., Rhopal. II., p. 174. Dr. Butler further distinguishes *Moschoneura*, Cist. Entom., Pt. iii.

The instance chosen by Fritz Müller was unfortunate. A wider view of Pierine affinities than he had the opportunity of taking would no doubt have led him to the conclusion that, after all, the original *Leptalis* probably was a white or white and black butterfly, and not a black and yellow or black and orange insect like *Leptalis* (*Dismorphia*) *melia*. Moreover, the position that *D. melia* is not a mimic can hardly be sustained. It bears a very considerable resemblance to *D. eumara*, which is itself an almost exact copy of *Actinote pellenea ; Actinote* being the neotropical representative of the well-known inedible genus *Acræa*. There is little room to doubt that *D. melia*, so far from preserving the primitive *Leptalis* type, has diverged to some distance therefrom under the influence of mimicry.

But although Fritz Müller's principal instance does not appear to me to be strong enough to bear the weight of argument that he rests upon it, there cannot be much question that his contention in the main is perfectly sound; and that, as a general principle, the process of mimetic assimilation depends rather on the development of old, than on the starting of new features, either of pattern or of colour.

In order to illustrate this principle, I have prepared the series of figures shown in Plates III. and IV., Figs. 1–12. These represent an array of facts that I venture to think are in many respects of great interest.

Fig. 1 shows the underside of the male of one of the ordinary neotropical non-mimetic Pierines*, a true *Pieris* as that genus is restricted by Dr. Butler—*P. locusta* of Felder. The chief points to be observed are in the hindwing. They are (1), the spots or patches of bright red which are found at the base of the precostal, median and internal spaces respectively (Fig. 1, *a*, *c*, *d*); (2) a well-defined yellow streak (*e*) occupying the costal space ; (3) a pale central area (*f*), in many specimens yellowish, occupying the region of the cell and the adjacent portion of the wing, especially towards the internal border; (4) a dark shade (*h*, *i*) on the anal and costal sides respectively of the pale central area. The present species happens to be a rather heavily coloured member of its group, but in other species of the same genus

* See below, p. 72, note.

Pieris we get a great lightening of the general tone of colour, without however losing the essential features now referred to. In *P. phaloe* for instance, also a non-mimetic *Pieris* from the same neotropical region, we have as it were an attenuated and washed-out version of the scheme of marking seen on the hindwing of *P. locusta.* Here (Fig. 2) are visible the same basal red patches, though now confined to the precostal and internal spaces; the same pale costal streak and central area, now in most specimens white rather than yellow; and on either side of the latter the same two dark shades, now reduced to a pair of brownish streaks. From either of these types to the well-known Heliconine form here represented by *Heliconius numata* (Fig. 11), seems a sufficiently long step; nor is it at first sight apparent that there is anything in common between the former and the latter schemes of coloration. Nevertheless, while it will be allowed on the one hand that the female of *Mylothris pyrrha* (Figs. 9, 10) presents a very good imitation of *H. numata,* it can be shown on the other hand that this last-named Pierine owes its mimetic features to a simple development of characters already possessed by the other Pierine forms just spoken of, to which it is closely allied.

In order to make this apparent, it will be necessary to refer to some of the other neotropical species of the same genus *Mylothris.* This interesting little group, comprising besides *M. pyrrha* the closely related *M. malenka, M. lypera,* and *M. lorena,* has been more than once spoken of by Mr. Wallace* as affording an instance of mimetic females associated with males of the ordinary white type of Pierine coloration. It is quite true that all the males throughout the group exhibit on their upper surfaces nothing but the ordinary white character; Mr. Wallace, however, does not mention the curious fact that the same males universally show on the under surface, though in varying degrees, an approach towards the Heliconine pattern that is so completely imitated by their mates. These partially developed features on the under surface of the males enable us to trace the history of the growth of the mimetic pattern.

Let us take the underside of the male of *Mylothris*

* "Tropical Nature," 1878, p. 204; "Darwinism," 1889, p. 271.

lypera (Fig. 3), and compare it with that of *Pieris locusta.* There is no difficulty in identifying the principal markings as before enumerated. The yellow costal streak and central area (*e, f*) and the anterior and posterior dark shades (*h, i*) are present in *M. lypera* as in *P. locusta,* all occupying the same relative positions; the precostal red however has disappeared, and the internal and median touches of the same colour have united and prolonged themselves into a triangular streak reaching about a third of the way across the wing (*cd*). A small dark area (*g*), which in *P. locusta* lies immediately posterior to the internal red patch, has in *M. lypera* extended itself in the same direction with the extension of the patch, and has, beyond the outer extremity of the latter, united with the anterior dark area (*i*) in such a way as to completely surround the red patch with a distinct region of black. All the areas somewhat vaguely indicated in *P. locusta* have in *M. lypera* acquired a distinct and definite character with sharply-marked, clear-cut borders. There is no doubt of the homology of the markings in the two cases, nor does the change from one to the other deserve to be called either violent or abrupt.

The underside of the male of *M. lorena* (Fig. 4) takes us a step onward. Here are exactly the same features, but with a further development along the same lines. The red patch has now become a definite streak reaching half-way across the wing, but still bears the same relation to the anterior dark area. The costal streak and central area have undergone a similar elongation, and in this instance are much paler in colour. The whole aspect perhaps recalls that of *P. phaloe* rather than that of *P. locusta,* and the correspondence with the former insect is still further borne out by the presence of a diagonal dark streak (*k*) in the forewing, part of which is indicated in *P. phaloe,* uniting the costal with the posterior or outer margin.

The general streakiness of the male of *M. lorena* is preserved or enhanced in the male of *M. pyrrha* (Fig. 5). There is in this case no diagonal dark band crossing the forewing, but the red streak of the hindwing acquires additional distinctness and importance, while the banded appearance is further increased by a slight change in the disposition of the enveloping black.

As far as the hindwing is concerned, we have now

all but reached the complete mimetic condition of *M. pyrrha* ♀ (Figs. 9, 10). The only thing still wanting is an infusion of more or less brownish red into the pale yellow or orange of the costal and central streaks. It is observable that even in the female *M. pyrrha* the assimilation between the old red of the basal patch and the new red of the costal and central areas is not quite perfect, the former always retaining on the under surface a more vigorous and decided tint than the latter (see Fig. 9, *e*, *cd*, *f*).

With regard to the forewing, there is no doubt a considerable interval between the male and female of *M. pyrrha*. An inspection, however, of the female of *M. lorena* and *M. malenka* (Figs. 6, 7, 8), enables us to see how it may be bridged over. Comparing the sexes of *M. lorena* (Figs. 4, 6, 7), we find that their patterns are identical in the main features, though the female has an additional dark streak in the forewing (*l*) running parallel with the inner border. The central pale area of the hindwing has also in the female almost or entirely disappeared from the lower surface, while the other spaces on both wings which in the male are white or very pale yellow, assume in the female a deeper yellow, warming towards the base of the wing to an orange or brownish red. These changes, comparatively slight as they are, are sufficient to give the female *M. lorena*, a decidedly Heliconine aspect. They point out, moreover, the manner in which the still more completely Heliconine facies of *M. malenka* ♀ (Fig. 8) and *M. pyrrha* ♀ (Figs. 9, 10) may grow naturally out of the Pierine materials already noticed. A very close comparison of *M. pyrrha* with *H. numata* (Figs. 10, 11) will indeed show that the correspondence of markings is not absolutely perfect in every particular; nevertheless, the general effect is marvellously alike, and if assisted by similarity in habits and mode of flight, must be amply sufficient for all practical purposes of protection to the *Mylothris*.

Looking at this series as a whole, and bearing in mind that it would be possible to include other forms * which would render the gradation still easier than is shown

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* For example, *P. marana* and *M. lypera* ♀.

here, we cannot, I think, feel any doubt that it is sufficient to demonstrate the possibility of the formation of a practically perfect mimetic pattern from the ordinary form of a quite distinct type, without any violent or abrupt changes of design. It does not, indeed, lend any support to the view that mimicry can only originate between forms that already possess considerable and obvious resemblance to one another, nor does it countenance the opinion that mimetic changes are effected *per saltum*. What the series of forms here figured does show is that, granted a beginning however small, such as the basal red touches in the normal Pierines, an elaborate and practically perfect mimetic pattern may be evolved therefrom by simple and easy stages.

II. Sexual Dimorphism in Mimetic Forms.

There remains, in regard to the foregoing series, a question of great interest; namely, what is the meaning of the diversity between the sexes in these more or less completely mimetic forms? Why should the one sex have advanced so much further along the mimetic path than the other? It is no doubt the case that the females stand in greater need of protection than the males, but to say this still leaves several questions unanswered. Are we right in regarding the male patterns as perpetuating stages through which the other sex has also passed in order to reach its present state of mimetic completeness, or are we to suppose that the selection by enemies has affected only the female sex, and that the patterns seen on the males are merely an incidental result of heredity, being, in fact, a secondary version of the female pattern transmitted in a weaker form? In either case, what has checked the further development of mimicry in the male? Is this imperfect development simply a passive result of the absence of necessity for change, or is there some active force at work preventing a further modification? It is well known that an explanation of a somewhat similar case has been sought in the principle of sexual selection; the females, it was suggested, as the more conservative sex, preferring in their mates the ancestral type of coloration of the group.* Mr. Wallace,

* Belt, "Naturalist in Nicaragua," Ed. 1888, p. 385.

on the other hand, points out that in the Pierine group before us the habits of the two sexes are different; that whereas the females haunt the forest glades in company with the Heliconii, the males congregate and fly in the open with other species of white butterflies, among whom a reddish or brownish insect would be especially conspicuous, and would be very liable to experimental tasting.* This fact would seem to supply an active check on the development of the pattern in the male, but it still leaves undetermined the meaning of so much of the Heliconine colouring as does exist, and of this Mr. Wallace has offered no explanation.

I am myself inclined to think that however much it may be to the advantage of these male forms to be taken under some circumstances for white butterflies of the ordinary kind, yet there must be times and occasions—probably while the insect is at rest and settled—when the partial mimicry of the underside comes into play, and tends to afford protection. An instance in support of this view exists in *Hesperocharis hirlanda* (Fig. 12). This insect, like the males of those that have just been considered, is on the upper surface an ordinary white butterfly of the usual kind; the lower surface, however, presents an incipient mimetic pattern of a like degree of development with those of *Mylothris lorena* ♂ and *M. pyrrha* ♂. This can be no feeble reflection of a mimetic pattern complete in the female, for the sexes of *H. hirlanda* hardly differ; moreover *H. hirlanda,* with one or two other forms probably not specifically distinct from it, is the only species of its genus which shows any approach towards a mimetic coloration. The mimicry, slight as it is, must therefore, it would seem, be of some service, as otherwise it would in this case be meaningless; and if this be so with *H. hirlanda,* it is reasonable to suppose that whatever amount of protection such an approach to the Heliconine pattern confers, is also shared by the males of *Mylothris.*

A further point of interest that arises in connection with *H. hirlanda* is this—that a mimetic effect which generally resembles that of *M. pyrrha* ♂, is here reached by different means. *Hesperocharis,* like *Mylothris,* starts no doubt from a regular Pierine form, such as that

* "Tropical Nature," 1878, p. 205.

exhibited by *P. phaloe*; but whereas in *Mylothris* the main red streak of the hindwing arises from the internal and median basal red, and is central (Fig. 5, *cd*), in *Hesperocharis* it results from a development of the precostal and costal red patches, and occupies the corresponding regions of the wing (Fig. 12, *a*, *b*). The precostal red is undeveloped in *Mylothris*, and the median red is undeveloped in *Hesperocharis*. One result of this is that in the latter form the relative position of the main yellow and red streaks is reversed; notwithstanding which the general resemblance to *Mylothris* is considerable, and the difference would very probably remain undetected by many insectivorous animals. The present point has already been noticed by me elsewhere.* I draw attention to it here simply because it affords another illustration of the gradual growth of mimetic patterns from an original non-mimetic form.†

III. Reciprocal Mimicry between Inedible Forms.

In the previous communication to the Entomological Society‡ of which I have already made mention, I drew attention to certain facts which I am now able to illustrate by Pl. V., Figs. 13 and 14, representing the undersides of a Pierine (*Pereute leucodrosime*) and a *Heliconius* (*H. melpomene*) respectively. Both *Heliconius* and *Pereute* are, it will be seen, furnished with basal red spots, and this is the case with very many of the *Heliconii* and their

* Trans. Ent. Soc. Lond., 1894, p. 286.

† Throughout the foregoing remarks, *P. phaloe* and *P. locusta* ♂, have been spoken of as non-mimetic forms. This is undoubtedly the case with *P. phaloe*, but it is perhaps possible that even in *P. locusta* ♂, the underside of the hindwing may have (especially in darkly-coloured individuals) a certain mimetic value. The underside of the hindwing in *P. locusta*, *P. cinerea* and some others resembles that of *Heliconius melpomene* and other protected species in giving the general idea of a dark wing-area with yellow costal or precostal streak and basal red spots. The forewing of *P. locusta* contains a large surface of white, but this would be partly or wholly concealed in the resting position. It is true also that the yellow streak and red patches do not occupy exactly corresponding positions in the *Pieris* and the *Heliconius*; but there is abundant evidence to show that while *affinity* displays great respect for the exact position on the wing of any given feature of the pattern, *mimicry* to a large extent disregards this, and aims rather at a general similarity of effect. See the instance of *Hesperocharis hirlanda* above, and see also below, p. 74, note.

‡ Trans. Ent. Soc. Lond., 1894, pp. 296, etc

Pierine imitators. What is the meaning of this coincidence? The first answer that suggests itself is that it is simply an ordinary case of mimicry; the red spots belong originally to the *Heliconius*, and the Pierine has acquired similar spots in order to complete the mimetic picture. Two facts, however, militate against this supposition. The first is that these red patches, so far from being confined to the mimicking Pierines, are found to have a very wide distribution throughout the whole Pierine subfamily, existing not only, as we have seen, in non-mimetic neotropical forms such as *Pieris locusta* and *P. phaloe*, but in numerous old-world genera as well, reaching a great development in the Indian and Australian *Delias*, and having even left a relic in the common white butterflies of our own country. It would be extravagant to suppose that these widespread characters owe their origin simply to the necessity for mimicking certain South American *Heliconii*. Moreover, as I have elsewhere shown, such an origin for the old-world forms as this hypothesis would involve is at variance with what is known of Pierine phylogeny. The second fact is that although several *Heliconii* which are not the subjects of mimicry show marks of the kind, yet they are most constant, most distinct and most Pierine-like in species of *Heliconius* that serve as models. There must, it would seem, be a relation between the two forms which is not entirely due to mimicry by the Pierine. Are we then to say that the *Heliconius* is the mimic and the Pierine the model? This would appear to be going against all received ideas on the subject, and to be negatived by all that is known of the inedible qualities of *Heliconius* and of the ancestral coloration of the Pierines; nevertheless, with respect to the particular marks in question I believe that it comes near to the true expression of the fact, and I would suggest that the key to the difficulty is to be found in the following considerations.

It has been well shown by Fritz Müller,* whose conclusions have been followed and amplified by Meldola and Poulton, that there exist two kinds of mimetic associations—in one of which an edible form shelters itself by resemblance to another form well known to be inedible, this being the aspect of mimicry first detected and explained by Bates; while in the other a group is constituted all of whose members are inedible, and join

* "Kosmos," 1879, p. 100.

forces, so to speak, in order to share the dangers of experimental tasting. In the first kind it is obvious that the only imitation must be by the unprotected of the protected form; there is no force tending in the converse direction. But in the second kind it does not seem to have been sufficiently noticed that, especially if the numbers of the associated species are approximately equal, there may fairly be expected to arise a kind of give-and-take arrangement, in consequence of which two or more inedible forms may hasten the assimilative process by imitating each other. This is my reading of the case before us. There are some independent grounds* for thinking that the mimicking Pierines in this particular group of instances are not, as has been generally assumed, edible. It is therefore not unreasonable to suppose that being distasteful, like the associated *Heliconii*, and forming with them a company for mutual protection, they have both taken from and bestowed on them characteristic features of pattern—both sides, in fact, having undergone what I some time since ventured to call "reciprocal mimicry." I have elsewhere given more detailed reasons in support of this view; I reintroduce it here for the sake of illustrating it from those Pierine marks that have been specially under consideration.†

* *E.g.*, (1) the abundance of some of the mimetic species of the same or of a closely allied genus, as *Pereute charops* and *Euterpe tereas* (testified to by Messrs. Godman and Salvin and by Fritz Müller respectively); and (2) the fact that the nearest old-world representatives of the same group, *i.e.*, the members of the genus *Delias*, have all the characteristics of insects protected by a disagreeable taste or odour.

† It may perhaps be objected that the resemblance between such forms as are represented in Figs. 13, 14 is not sufficiently close to warrant the supposition of mutual protection between them. To this it may be replied, that (1) the colour of the diagonal band of the forewing is probably in the living *Heliconius* much nearer to that of the *Pereute* than appears in the figure, which was taken from a specimen that had been for some years in the Hope collection. It is well known that the reds in *Heliconius* and *Acræa* are especially apt to fade on keeping. (2) The resemblance may be enhanced by attitude, the figures having been drawn without any particular attention to this. (3) The brightly coloured basal marks, though occupying different relative positions in the two insects, convey the same general idea of a gently-curving, slender, white or yellow streak (belonging to the forewing in the *Pereute* and the hindwing in the *Heliconius*), beset near its base with isolated spots of vivid red, and traversing a black or dark-brown area of wing close to the body.

The same argument will apply to features similar to the above which may be seen in certain *Papilioninæ*, *Nymphalinæ*, *Erycinidæ*, and even in some moths. And I may say in passing that Fritz Müller's principle here referred to appears to me to be of much wider application than has been hitherto supposed. There exist several large groups more or less uniform in their scheme of coloration, though heterogeneous in their affinities, which it seems almost certain will in the main turn out to be cases of "inedible associations," each one possibly including a few instances of true mimicry within its borders. In deciding on the actual nature of such resemblances, it may be borne in mind that "reciprocal mimicry" constitutes good evidence of the distastefulness of all the forms between which it can be shown to occur, while the abundance or scarcity of a mimetic insect is also a valuable test of its edibility.

IV. Divergent Members of an Inedible Group.

The last set of figures (Pl. V., Figs. 15–18) discloses a remarkable state of things, which is of interest both in its bearing on what has been advanced in the preceding section, and also as providing a further illustration of the importance of small changes. The *Papilio* represented in Fig. 15 (*P. zacynthus* ♀) is undoubtedly the model for the Pierine shown in Fig. 16 (*E. tereas*). These two insects form one of Bates's original instances of mimicry. But beside the latter we have another *Euterpe*, viz., *E. bellona* (Fig. 17), whose markings are, without doubt, homologous with those of its congener. *E. bellona* however, though so closely resembling *E. tereas* the mimic of *P. zacynthus*, itself copies, not the *Papilio*, but the members of a group of *Heliconius* of which *H. erato* (Fig. 18) is a good example. The bright yellow patch on the forewing of the *Heliconius* is very well imitated by the Pierine, and on the hindwing of the latter the crimson patch of *E. tereas*, etc , has been modified into a series of scarlet stripes; these being a palpable attempt to reproduce the radiating chestnut streaks of *H. erato* or one of its congeners. It is curious to see what slight modifications between the two species of *Euterpe* enable them to

imitate two such distinct insects as the *Papilio* and the *Heliconius*.*

The addition of these two forms, viz., *Euterpe bellona* and *Heliconius erato*, the former of which was perhaps not known to Bates, evidently complicates the "mimicry" question. Is the resemblance between the *Heliconius* and the *Papilio*, which certainly exists though it is not very close, accidental? But for the intermediate Pierine forms we should perhaps not have suspected any special relation between them. On the other hand, is the *Heliconius* the general model for all the rest? If so, *P. zacynthus* becomes a mimic instead of a model; while its own imitator, *E. tereas*, is in the curious position of mimicking a mimic, instead of going straight to the fountain-head, *i.e.*, the *Heliconius*.

In my opinion, the most satisfactory way of accounting for these complicated relations is the supposition that here we have another instance of a mimetic assemblage of the second kind—an "inedible association." The two extreme forms, viz., the *Papilio* and the *Heliconius*, which by themselves might perhaps not be sufficiently near one another to be mutually protective to any very great extent, are held together, as it were, within the limits of an inedible mimetic group, by the welding power of the intermediate *Euterpes*.† It is of interest in connection with what has been already advanced as to reciprocal mimicry, or the give-and-take system, in associations of this kind, that the *Papilio*, the *Heliconius* and both Pierines are furnished on the underside with basal red spots.

V. Conclusion.

It cannot, I think, be doubted that the remarkable facts touched upon in the present paper raise points of fresh interest in the great question of mimicry. The leading and binding idea in all that I have said has been

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* The Heliconine pattern is still further developed in the female, and on the under surface of the male of *E. bellona*, than on the upper surface of the latter sex as represented in Fig. 17.

† The series could be rendered still more complete by the insertion of *E. critias* and *E. bellona* ♀, on the *Papilio* and *Heliconius* sides respectively of *Euterpe bellona* ♂.

my conviction, formed after much deliberation, of the gradual and natural character of these complicated changes, and of the absence of any violent or arbitrary element in their process of development. Whether the explanations here suggested are true and adequate, can in most instances only be decided by observation in the field; and it is much to be desired that travellers and residents in countries where these and similar phenomena occur should carefully record all facts relating to the habits, postures, modes and times of flight, prevalence, seasonal occurrence and exact distribution of the various species that come under their observation.

There is also need of such experimental evidence as to the means of defence adopted by these forms as can only be satisfactorily obtained in the midst of their natural surroundings. Meanwhile, it must suffice to point out the conclusion towards which the only facts available appear to lead, while the actual verification by observation and experiment must perforce be left to those whose opportunities enable them to apply these final tests to the subjects of enquiry.

My best thanks are due to Prof. Poulton, F.R.S., for much encouragement and many facilities for work. The figures were drawn, by his permission, from specimens in the Hope Collection at Oxford.

List of Species mentioned.

Pierinæ.

Pereute leucodrosime, Koll.
Euterpe tereas, Godt.
,, *critias*, Feld.
,, *bellona*, Cram.
Mylothris pyrrha, Fabr.
,, *lorena*, Hew.
,, *lypera*, Koll.
,, *malenka*, Hew.
Hesperocharis hirlanda, Stoll.
Pieris locusta, Feld.
,, *phaloe*, Godt.
,, *marana*, Doubl.
,, *cinerea*, Hew.
Dismorphia melia, Godt.
,, *eumara*, Doubl.

Papilioninæ.

Papilio zacynthus, Fabr.

Acræinæ.

Actinote pellenea, Hübn.

Heliconinæ.

Heliconius melpomene, Linn.
,, *erato*, Linn.
,, *numata*, Cram.

EXPLANATION OF PLATES III., IV., & V.

PLATE III.

FIG. 1. *Pieris locusta* ♂, underside.
2. *P. phaloe* ♀, „
3. *Mylothris lypera* ♂, „
4. *M. lorena* ♂, „
5. *M. pyrrha* ♂, „
6. *M. lorena* ♀, „

PLATE IV.

FIG. 7. *Mylothris lorena* ♀, upperside.
8. *M. malenka* ♀, „
9. *M. pyrrha* ♀, underside.
10. *M. pyrrha* ♀, upperside.
11. *Heliconius numata*, upperside.
12. *Hesperocharis hirlanda*, underside.

PLATE V.

FIG. 13. *Pereute leucodrosime*, underside.
14. *Heliconius melpomene*, „
15. *Papilio zacynthus* ♀, upperside.
16. *Euterpe tereas*, „
17. *E. bellona* ♂, „
18. *Heliconius erato*, „

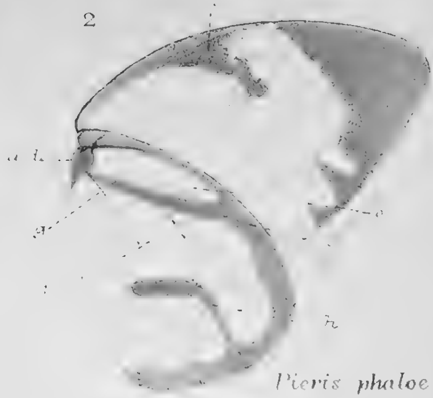
IN ALL THE FIGURES

a, precostal red patch on the base of the hindwing underside.
b, costal „ „ „ „
c, median „ „ „ „
d, internal „ „ „ „
e, costal light streak.
f, central pale area.
g, *i*, anterior dark shades.
h, posterior dark shade.
k, diagonal dark bar of forewing.
l, dark bar of forewing parallel to inner margin.

1

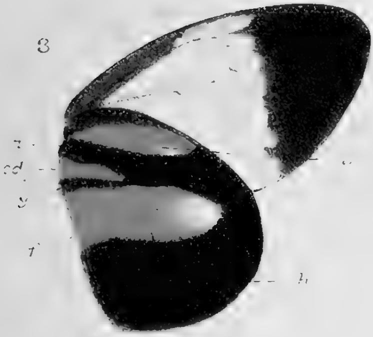
Pieris locusta ♂
under side

2



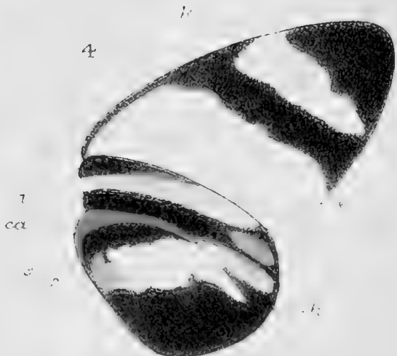
Pieris phaloe ♀
under side

3



Mylothris hypera ♂
under side

4



Mylothris lorena ♂
under side

5

Mylothris poppea ♂
under side

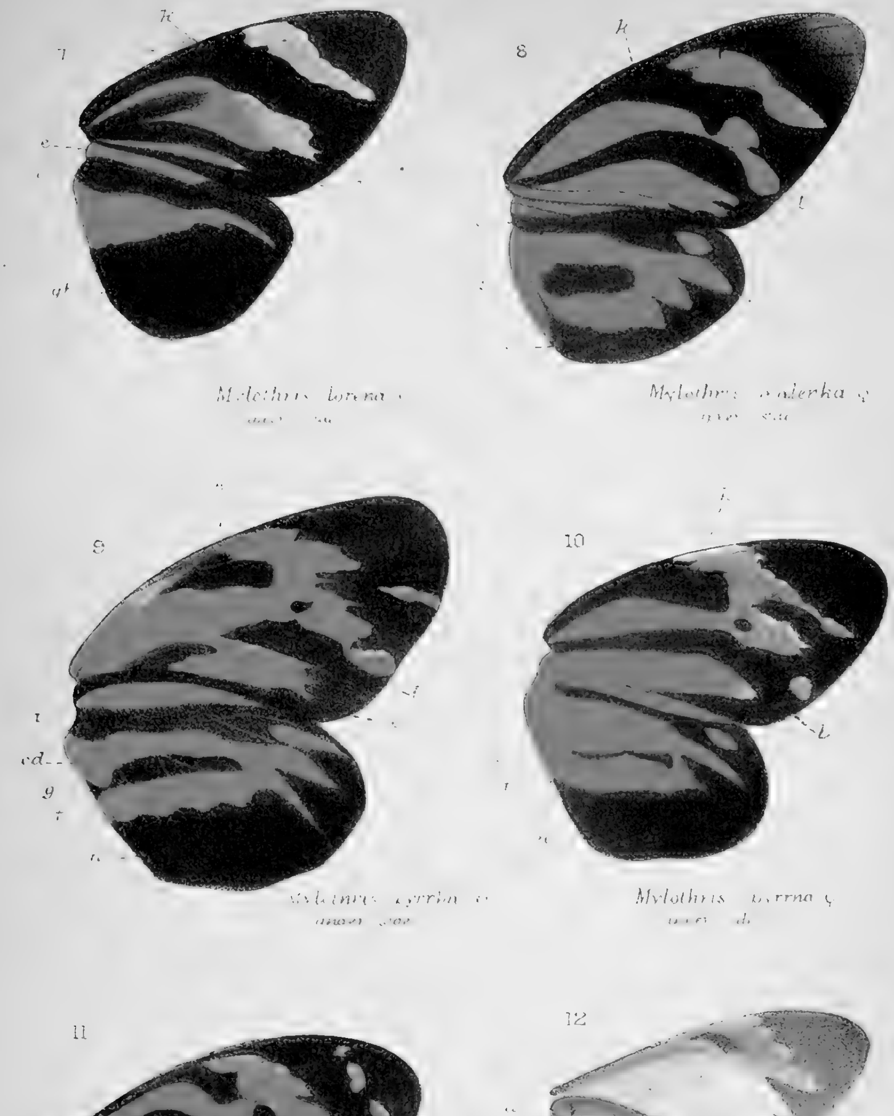
6

Mylothris lorena ♀
under side

C.A. Lixey pinx.

West, Newman chromo.

Growth of Mimetic Patterns



Mylothris lorena ♀
upper side

Mylothris ?alerka ♀
upper side

Mylothris pyrrha ♂
upper side

Mylothris ...rrna ♀
under side

Heliconius ...
upper side

Hesperocharis ...
under side

F.A.Dixey pinx^t

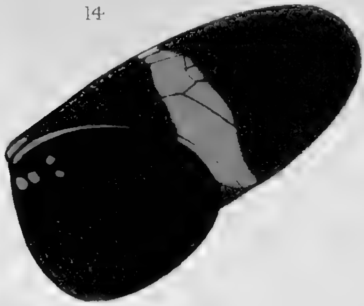
West, Newman ...

Growth ... Patterns

13

Pereute leucodrosime
under side

14



Heliconius melpomene
under side

15

Papilio zacynthus ♀
upper side

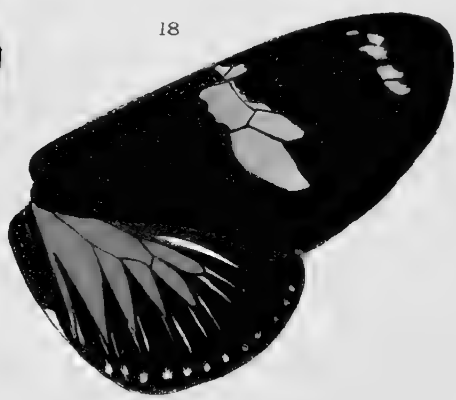
16

Euterpe tereas
upper side

17

Euterpe bellona ♂
upper side

18



Heliconius erato
upper side

P.A.I... pinx^t

West, Newman chromo.

Mimetic Patterns
(Müllerian Groups.)

IX. *On the Phylogeny of the* Pierinæ, *as illustrated by their Wing-markings and Geographical Distribution.* By Frederick A. Dixey, M.A., M.D., F.E.S., Fellow of Wadham College, Oxford.

[Read February 7th, 1894.]

Plates III., IV., V.

Table of Contents.

I. Introductory.

In the present paper my object has been to apply to the study of the subfamily *Pierinæ* the methods which I used in investigating the phylogenetic relations of another group of Lepidoptera, as recorded in a former communication to this Society.* I have in the first place endeavoured to work out the homology of the various

* "On the Phylogenetic Significance of the Wing-markings in certain genera of the Nymphalidæ," Trans. Ent. Soc. Lond., 1890.

markings to be found throughout the group, and have then attempted to state the phylogenetic conclusions to which this evidence appears to lead. Though my principal aim has been the elucidation of the Pierine wing-markings, which so far as I am aware have never before been systematically studied from this point of view, I have not ignored those other features that are usually known as "structural"; and I have also tried to estimate the bearing upon phylogenetic questions of the facts relating to the present distribution of the *Pierinæ* in space. The serious limitations under which anyone who wishes to construct a phylogeny for such a group as this must necessarily labour have been elsewhere acknowledged; it is of course manifest that little or no help can be expected from embryological or palæontological sources. There are, however, many compensating features to be reckoned on the other side; and in view of certain comments that have at times been passed on previous work of this kind, I may perhaps be allowed to quote a few sentences from the writings of one of our leading naturalists, which seem to me to state the special advantages afforded by these and similar researches with a force and cogency that it would not be easy to gainsay. After pointing out the pre-eminent value of the Diurnal Lepidoptera to the student of distribution and variation, the writer I refer to proceeds as follows—"But besides their abundance, their universal distribution, and the great attention that has been paid to them, these insects have other qualities that especially adapt them to elucidate the branches of inquiry already alluded to. These are the immense development and peculiar structure of the wings, which not only vary in form more than those of any other insects, but offer on both surfaces an endless variety of pattern, colouring, and texture. . . . This delicately painted surface acts as a register of the minutest differences of organization,—a shade of colour, an additional streak or spot, a slight modification of outline continually recurring with the greatest regularity and fixity, while the body and all its other members exhibit no appreciable change. The wings of butterflies, as Mr. Bates has well put it,* 'serve as a tablet on which Nature writes the

* See "The Naturalist on the Amazons," 2nd edit., p. 412.

story of the modifications of species'; they enable us to perceive changes that would otherwise be uncertain and difficult of observation, and exhibit to us on an enlarged scale the effects of the climatal and other physical conditions which influence more or less profoundly the organization of every living thing."* Whether any particular investigator is or is not competent to undertake this kind of research may be open to question, but I think that the study itself needs no further vindication than these words of Mr. Wallace.

In treating of the details of the wing-markings I have tried to be intelligible and explicit, even at the cost of being somewhat lengthy. I have, however, been obliged to content myself with selected examples; a complete treatment would run to a vast length, and in most cases the lines here laid down may be easily applied to the insects not mentioned in this paper. Some of the identifications of markings may at first sight seem startling; for instance, that of the straight orange-coloured line crossing the disc of the wings in *Dercas* with the series of black spots in the females of *Ganoris*; but I believe that in every such case it will be found that the homology can be certainly traced, step by step. It is hardly necessary to point out the importance of being on one's guard against the misleading suggestions of merely superficial resemblances, and also of giving due weight to the disturbing influence of mimicry. The details of this latter process, when minutely examined in a favourable group such as the *Pierinæ*, are seen to be of so complicated and interesting a character, that I may hope to be excused for having treated of some of these details with considerable fulness, and even for having ventured to introduce a new term in order to distinguish a special case of the phenomenon known as "Convergence."†

The generic names employed in this paper are those of Mr. Butler in his well-known "Revision" (Cistula Entomologica, vol. i., 1870, p. 33), supplemented by subsequent memoirs from the hand of the same author, and

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* "On the Papilionidæ of the Malayan Region," Trans. Linn. Soc., xxv., p. 1 (1866).

† See page 298.

by the arrangement at present adopted in the National Collection under his charge. I confess that I am not always in agreement with this arrangement, but the importance of a definite and accessible standard is obvious, and no better one could be found for my purpose. Even if the genera are not in every instance distinguished by characters of real "generic value," they are usually natural groups, and in most cases of great convenience in practice. The list of genera and species which I have appended may be found useful as indicating the exact insects which are mentioned in the course of the paper, and also as giving an idea of the scope and contents of those genera whose names may still be somewhat unfamiliar. A paper of this kind is not the place in which to introduce changes of nomenclature or to discuss questions of synonymy; and as regards classification I have done no more than throw out a few suggestions which, perhaps, may one day be taken up.

II. The Wing-markings.

1. *The submarginal series of dark spots.*

Comparing together the three species of the subfamily *Pierinæ* that are commonest in this country, viz., *Ganoris brassicæ, G. rapæ,* and *G. napi,* we find that the females of all three resemble one another in the possession of a series of black spots on the upper surface of the forewing. One of these spots (Fig. 16, S 8) occurs between the second and third median nervules; another (ibid., S 10), between the first median nervule and the submedian nervure; and the third (ibid., S 11) between the submedian nervure and the inner margin of the wing. The latter spot, which varies considerably in the amount of its development, takes the form of a streak nearly parallel with the inner margin. In the males, this series of spots is evanescent. The whole series is normally absent in *G. brassicæ* ♂, and in some specimens of *G. rapæ* ♂, and *G. napi* ♂; the males of the two latter species, however, generally have the spot between the second and third median nervule more or less developed, though the other two are not present. Turning to the underside of the wing in these species, we find the first two spots usually present in both males and females;

the third is but faintly visible in the female, and in the male not visible at all. These three spots are all that can be seen in ordinary specimens of *G. brassicæ, rapæ,* and *napi;* but in some specimens of *G. napi,* and less distinctly in some of *G. rapæ,* the series is continued towards the anterior border of the wing by a fourth spot placed just behind the junction of the third and fourth subcostal nervules, and traversed by the first discoidal. The spots that have now been referred to can be seen in a very well-marked form in *G. gliciria.*

These indications of a submarginal series of black markings become more pronounced in *Synchloe daplidice.* Here, in the female, a submarginal row exists in easily recognisable form, three of the constituent spots of which are clearly homologous with those already described in *G. napi, rapæ,* and *brassicæ* (Fig. 15). In this region of the wing nearly every interspace between nervules contains a spot; the spots tending to become confluent, especially towards the costal margin. There is generally no spot between the first and second median nervules, and often none between the submedian nervure and the inner margin of the wing. In the male, the anterior portion of the series is distinct enough, the large spot, however, between the submedian nervure and first median nervule is absent from the upper surface, though regularly present beneath. The female *S. daplidice* also shows a continuation of the same series on the hindwing, well-marked at the costa, but usually becoming less plain as the anal angle is approached. In the male *S. daplidice,* one term of the series is generally all that is present in the hindwing; and turning back to *G. brassicæ, rapæ,* and *napi,* we find the same spot invariably present on the upper, and often on the lower surface of the costa in the hindwing of both sexes (Figs. 15, 16, S 14—18).

Other species of the genus *Synchloe* present the same submarginal series in greater completeness. *S. callidice* ♀, for instance, has the whole series well developed on the forewing, and in most specimens on the hindwing also. A comparison with *S. daplidice* will show that the series is really homologous in the two cases, and will, moreover, demonstrate that in *S. callidice* the smallest spot of the series belongs to the interspace between the first and second median nervules, which in *S. daplidice* is usually

not furnished with a spot at all; and that the largest and best-marked member of the group, namely that between the second and third median nervules, corresponds with the spot which we saw to be most persistent in the males of *G. brassicæ*, *rapæ*, and *napi*. This spot, moreover, as well as the next most persistent (that between the first median and submedian), is usually picked out with black on the underside of both *S. callidice* and *S. daplidice*, where the markings corresponding to those of the upper surface are, as a rule, chiefly composed of green or yellow scales with but small admixture of black. The hindwing of *S. callidice* ♀ shows a continuation of the series; though here the markings as they approach the inner margin tend to assume the appearance of chevrons rather than of spots, which tendency is still more marked on the underside.

The South American genus *Tatochila* presents the same series on both fore and hindwings, the females as a rule most completely (as in *T. autodice*). The male of *T. theodice*, however, exhibits the whole series quite plainly; and in both of these species the markings in question tend to assume the form of a line of chevrons, the apices of which point towards the margin of the wing, instead of towards the base, as in *S. callidice*.

I propose to distinguish this series of spots as S (for Submarginal), numbering the constituent markings according to the interspaces they respectively occupy. In all the forms as yet mentioned the full number of marginal interspaces, from the costal nervure to the anal angle, is in the forewing 11, in the hindwing 8. Another space may be reckoned in the hindwing, that, namely, between the costal margin and the costal nervure. The corresponding space in the forewing is exceedingly narrow, and never carries a separate spot. We may take then the number of spaces potentially containing spots as 11 and 9 in the fore and hindwing respectively, and may designate all possible terms of the series as S 1—20, beginning at the costa of the forewing. None of the species above referred to exhibits the whole range of spots from 1 to 20 in a discrete condition, some being generally absent and others fused; the series may, however, be seen complete on the upper surface of the forewing and lower surface of the hindwing in many specimens of *Callidryas philea* and *C. thalestris* ♀ (Fig. 22, S 1—11).

In certain genera (*Eronia, Euchloe,* etc.), the presence of a fifth subcostal nervule gives rise to an additional interspace in the forewing; this, however, causes no difficulty, inasmuch as the extra interspace so formed is never occupied by a distinct spot. If necessary, the additional subcostal interspace may be referred to as 5a; by which plan we shall avoid throwing the numbering out of correspondence with that adopted in the other genera (see Fig. 23). In those genera (*Pereute, Delias,* etc.) which possess only three subcostal nervules in the forewing, I shall for convenience consider S 4 as absent.

Having identified the series S in the species named, we shall find no difficulty with the remaining members of the genera *Synchloe* and *Tatochila,* all of which possess it in a condition of greater or less development. In all these cases, if the sexes differ, the female invariably presents the series in greater completeness; though such of the spots as are present in the male are sometimes more distinct. Thus in *S. hellica* ♀, the whole range occurs with the exception of S 9 (this being also the spot which is regularly small or absent in *S. callidice* and *S. daplidice* ♀), and the spots show a great tendency to fuse into a submarginal band, especially towards the costa of the forewing. In the male, however, all are absent from the hindwing, and S 9—11 also from the forewing; S 8 is distinct; S 7 hardly visible; and S 2—5 are fused into a single spot which is more distinct than the corresponding patch in the female.

The same submarginal series can be traced with equal certainty in the genus *Belenois.* Here again the series is as a rule more complete in the females, while the individual spots are more distinct in the males. This can be well seen for example in *B. mesentina* (Fig. 13), where the males show a submarginal band on the forewing which can without difficulty be resolved into a series of five spots, representing S 2—3, 5, 6, 7 and 8. On the upper surface of the females the spots show a greater tendency to fuse with one another, and with the dark area of the apex and hindmargin; they are nevertheless in most specimens recognizable on the upper surface, and nearly always fairly distinct beneath. Much the same is the case with the submarginal series on the hindwing; this is constantly present in a distinct form on the under surface of both

sexes, and also to a variable extent on the upper surface of the male. The whole range (except the last member, S 20) occurs constantly on the upper surface in the female, but shows a strong tendency to fuse with the dark marginal band of the wing. In both male and female of this species the conspicuous and persistent spot S 8 occupies a prominent position, being pushed back as it were towards the centre of the wing, and so causing an indentation in the submarginal row. In *B. severina* the series is generally less well-marked than in *B. mesentina*, being to a great extent fused with the dark marginal band; S 10 and 11, however, which are absent in the latter insect, are mostly visible in *B. severina* ♀. *B. calypso* is noticeable as having the present series particularly well-marked on the underside of the hindwing; in the female it is also well in view on the upper surface. *Pinacopteryx larima*, again, has the series well developed on the hindwing, and recalls some species of *Synchloe* and *Ganoris* by the prominence given to S 8, 10, and 11. In several species of *Belenois*, as for instance *B. teutonia* ♀ and *B. coronea*, the fusion of the spots of series S with one another and with the dark apical and marginal area is almost or quite complete. (See *B. peristhene*, Fig. 14).

The genera *Appias*, *Catophaga*, and *Hiposcritia* present us in many of their members with the same series, more or less developed. In *H. lalage*, for instance, S 1—9 are fairly well marked on the forewing (most distinctly on the underside); while some spots of the series are also in most cases visible on the hindwing. In the greater number of species, however, the series is so fused with the dark apical and marginal area as to be hardly distinguishable (as in *C. zamboanga* ♀), or is altogether obsolete (as in most specimens of *A. nero*). It is noticeable that the spot S 8, to which I have before drawn attention, is usually the last to disappear from the forewing; and that in many cases where S no longer exists as a separately recognizable series, the place of S 8 is indicated by a prominent projection inwards of the fused marginal area (Figs. 9, 10, 11). The underside of the hindwing often retains traces of the submarginal series when the upper surface of one or both wings has entirely lost them (*C. lankapura* ♀ and some specimens of *A. nero*).

In the genus *Delias* the same assemblage of spots meets us again, though scarcely in a very definite form. The well known *D. eucharis* (Fig. 5) shows the series on both surfaces of each wing, the spots being to a great extent merged with one another; the band formed by their fusion is nevertheless quite distinct, and its indentations correspond with the usual disposition of the spots on the wing in those species where they exist in a more discrete condition. The series is also visible in *D. hyparete* (underside); and the same range of markings is present as a sinuous band in the Australian *D. aganippe* (best seen in the female, and on the underside); in less distinct form in *D. harpalyce*, and still recognizable, though now almost completely merged, in the closely allied *D. nigrina*. A comparison of the upper surface of the wings of the last named insects with those of other species of the genus *Delias*, such as *D. belladonna* (Fig. 4), *D. pasithoe*, and *D. thisbe*, serves to suggest the manner in which the submarginal series (in common with other features) may have arisen—namely, as a survival of an original dark ground-colour, which has become broken up, first into irregular bands and finally into spots, by the appearance and gradual enlargement of touches of a lighter colour in the spaces between the nervules. Further reference will be made to this point when other markings, whose history appears to be similar to that of the present series, come under consideration.

Metaporia agathon (Fig. 7) presents the series in much the same condition as *D. eucharis*, the band is, however, somewhat thicker and less defined. It is easy to trace the same feature through many species of the genera *Pontia* and *Huphina*; thus in *P. soracta* it is met with in the hindwing as a series of faintly-developed acute-angled chevrons, pointing outwards (as in *Tatochila*). In the forewing, S 3, 5—9 are easily visible. It is noticeable that S 8 is in this insect exceptionally small; it retains, however, its usual tendency to break the line of the series by advancing further than the others towards the centre of the wing. In *Pontia cratægi* the whole series has vanished; but in *Huphina coronis*, *H. phryne* (Fig. 8) and others, it is well marked; the most persistent spots being, as in other genera, S 6, 8 and 10; and the same general differences between the sexes, in relation to the series, being observable here as in *Synchloe*

and *Ganoris*. Indications of the series, more or less pronounced, can also be seen in *H. timnatha, H. aspasia, H. judith, H. nama*, and other species.

The strong resemblance to *Delias belladonna* borne by *Prioneris thestylis* is very probably due to mimicry, as suggested by Wallace ("Pieridæ of the Indian and Australian Regions," Trans. Ent. Soc. Lond., 3rd series, iv., pp. 309, 383). But from the presence of traces of the submarginal series in other species of *Prioneris* (as in *P. autothisbe* and *P. clemanthe*), it seems likely that it is rather the retention than the origin of the submarginal series in *P. thestylis* that is attributable to this cause. Material for the production of a likeness of *D. belladonna* was no doubt already to hand in the existence of an homologous series of markings in both insects. Other species of *Prioneris*, not having the same reason for keeping close to the original design, have strayed away more or less widely from it.

Mr. Wallace has also pointed out the agreement in some respects between *Delias* and the South American genus *Euterpe* (ibid., p. 344). If, with Mr. Butler, we divide Swainson's genus *Euterpe* into *Pereute, Leodonta, Catasticta* and *Euterpe* proper, we shall find that while all the normally coloured species of the group are demonstrably linked with one another and with *Delias* by their general system of marking and scheme of coloration, two of the genera (*Pereute* and *Leodonta*) further suggest a near relationship with *Delias* by the peculiarities of their neuration; there being in these instances only three instead of four subcostal nervules in the forewing (Butler, "Revision of the Genera of the Subfamily *Pierinæ*," Cistula Entomologica, vol. i., 1870, pp. 39, 40, etc.). The appearance of several species of this group of genera (notably *Euterpe tereas*) has been profoundly altered by mimicry; but putting aside such forms as these, we shall find no difficulty in tracing a common pattern throughout most of the remaining members of the group. This pattern is not dissimilar from that which characterizes those species of *Delias* which we have seen to be probably the older (*e.g.*, *D. belladonna, D. pasithoe* and *D. thisbe*). To this part of the subject I shall return later, at present it will be sufficient to point out the distinct presence of the submarginal series S in such examples as *Catasticta*

nimbice, *C. anaitis*, *C. bithys*, and to a less degree in *Leodonta dysoni* and *L. tellane*. The close resemblance between the remarkable Pierine *Eucheira socialis* and *C. bithys*, in respect of the marking of the upper surface, may warrant us in identifying the corresponding portion of the wing in the former insect with the submarginal row S undoubtedly present in the latter (Figs. 1, 2).

The series S having now been traced through several genera, until it, so to speak, loses itself in such generalised, and apparently primitive forms as those presented by *Delias belladonna*, *Catasticta bithys* and *Eucheira socialis*, it will be advisable to return to the genus *Synchloe*, and seek thereabouts for a new starting-point from which to pursue the same series through its developments in a fresh assemblage of genera which have not at present been noticed. Such a starting-point may be found in a comparison of *S. daplidice* ♀ with the female of almost any species of the genus *Colias*. A short examination will show that the same submarginal series exists in the latter genus. A good species for the purpose is *C. hyale* (Fig. 20), in which both sexes exhibit the series distinctly. The constituent spots broaden out towards the costa and tend to become fused with one another and with the black patch at the apex. This tendency is carried further in many species of *Colias*, particularly in the males, where, as in *C. edusa*, marginal and submarginal markings are fused together into a deep dark border. The females, however, preserve the spots of the submarginal series in a more discrete condition. In most species of *Colias* S is well developed on the under surface, the component spots being usually black on the forewing, and on the hindwing orange or pinkish. In a few species, such as *C. phicomone* and *C. palæno*, the series is obscured or absent. *Meganostoma*, which resembles *Colias* so closely in other respects, shows also the submarginal series on the under surface; usually as a row of somewhat faint pinkish dots, which are clearly identical with S in *Colias*.

Through *Meganostoma* the passage is easy to *Gonepteryx* and *Amynthia*. In *G. rhamni* and *G. cleopatra* no vestige of S is to be seen on the upper surface; on the lower surface, however, of many of the males and most

of the females, it is visible in the hindwing, and near the apex of the forewing, as a series of minute brownish dots; similar to, but as a rule even smaller than, those of *Meganostoma*. *Rhodocera leachiana* and *Amynthia mœrula* show exactly the same feature, the spots being dark brown or black, and a vestige of the series is present in *A. clorinde*. In the closely-allied genus *Dercas*, S is curiously modified into a brown or orange streak passing in an almost straight direction from the apex of the forewing to the anal angle of the hindwing. In *D. wallichii*, S 8 is large and prominent; but the remainder of the series is scarcely visible on the upper surface, though easily recognisable below.

In the genera *Callidryas*, *Catopsilia*, and their allies, the extent to which S is developed varies within wide limits. *Callidryas philea* ♀ has already been noticed as presenting, on the upper surface of the forewing, in many specimens, a complete set from S 1 to S 11 (Fig. 22). In this, as in other species of the genera named, it is usually S 7 and not S 8 that breaks the line by advancing towards the centre of the wing. The series is not usually continued on the upper surface of the hindwing, but both wings show it tolerably well below. S is well developed on the upper surface of *Catopsilia flava* ♀ (Fig. 21), and is visible to a variable extent on both surfaces (except the upper surface of the male) in *C. catilla*, *Aphrissa godartiana*, and others. In some of these insects S on the under surface forms part of the characteristic brown or pinkish mottling of the wing; in others, as the male of *C. phlegeus*, it is almost or quite reduced to the condition of minute pink spots, like those of the genus *Gonepteryx*. It is worth noticing that on the underside of *Phœbis trite*, S takes in the forewing the form of a straight streak, not unlike that in *Dercas lycorias*, leading diagonally across the wing. On the hindwing a similar streak appears, which, however, does not represent S as the apparently corresponding streak in *Dercas* undoubtedly does, but is at least partly developed from another system of spots which will be noticed later. Attentive examination will disclose the existence of traces of the true S between the streak in question and the hind border of the wing.

In *Hebomoia* the series is always at least partly visible on the forewings, and often on the hindwings as well.

The component spots are usually large and distinct, as may be especially well seen in *H. glaucippe* ♀ (Fig. 19). The same insect also shows the series tolerably well on the under surface, where it is in other members of the genus, as a rule, somewhat lost in the general mottling of the wing.

S is often well seen on the underside of species belonging to the genus *Ixias*, where it assumes a condition very like that which obtains in *Colias*. In *I. marianne* it is especially well developed, and the component spots on the hindwing are often furnished with pale centres. Some members of the series are frequently also visible on the upper surface, as in *I. marianne* ♀, where S 6—9 are conspicuous (Fig. 18).

The genera *Teracolus*, Swains., *Idmais*, Boisd., and *Callosune*, Doubl., are united by Mr. Butler as *Teracolus*. In most of the species included under this head, the series now being discussed is distinctly visible, especially in the female and on the under surface. Good examples of the series are furnished by *T. danae* and *T. etrida*. In *T. eucharis* ♂ it has mostly vanished from the upper surface; S 8, however, remains, as in so many other instances, and is, moreover, in this insect often reinforced by the presence of S 13 and 14, which spots have been also seen to persist in our common species of *Ganoris*. The female of *T. regina* possesses S in a well-developed condition on both surfaces, S 10 being especially conspicuous. The same series is visible to a less degree in the female of *T. ione*. The males of both species show indications of S on the lower surface, but none on the upper. The series may also be seen in a well-developed state in *T. hewitsonii* and *T. amata* (Fig. 17).

In *Euchloe* the series has almost disappeared. A relic, however, persists near the apex of the forewing in some species, best seen, perhaps, in *E. tagis*, *E. ausonia*, and *E. hyantis*; while *E. reakirtii* ♀ shows S on the upper side of the forewing very distinctly; S 8 indenting the line as in the genus *Synchloe*. A comparison of the under surface of the hindwing in *E. cardamines* and *E. eupheno* with the somewhat similar system of marking in *S. daplidice* suggests also the probability that part of the green mottling in *Euchloe* represents the submarginal series. The same series is certainly visible on the upper surface of the hindwing in some specimens of *E. lucilla* ♀.

Certain species of *Nepheronia*—for example, *N. jobœa* ♀ and *N. valeria* ♀—show the series S in a form that strongly recalls the condition of the same series in *Metaporia agathon*. In both *Nepheronia* and *Eronia*, however, S is very apt to be merged, especially on the upper surface, with the dark marginal area. The female of *E. leda* (Fig. 23) shows the first few spots of the series on the upper side of the forewing in a condition resembling that in some species of *Callidryas*, which resemblance applies also to the lower surface, where S occurs in a modified form on both wings, traces of the same series being likewise visible in the male.

Summary.—Most of the members of the subfamily *Pierinæ* possess, in a greater or less state of development, a submarginal series of dark spots. The genera *Synchloe*, *Belenois*, *Tatochila*, and some species of *Colias*, amongst others, present the series in a fair state of completeness. In other members of *Colias*, and in several genera such as *Ixias*, *Hebomoia*, and *Teracolus*, the series is often less distinguishable, owing either to fusion of its constituent spots with each other and with the dark marginal area, or to suppression of some of their number. Relics of the series remain in *Ganoris*, *Euchloe*, and other genera, being especially persistent in the female sex; in *Gonepteryx*, *Dercas*, *Callidryas*, *Phœbis*, *Catopsilia*, and other allied genera, the series often undergoes curious modifications. The aspect of the series in such genera as *Pontia*, *Huphina*, *Metaporia*, and *Nepheronia*, suggests its development from portions of the original ground-colour left (by the formation and subsequent fusion of lighter patches in a dark or dusky area) as a dark band following the contour of the wing; and, finally, by an extension of the process, as a submarginal chain of spots. The possibility of such a mode of origin is well illustrated by the condition of the wings in many species of the Eastern genera *Prioneris* and *Delias*, and the Western *Leodonta*, *Catasticta*, and *Eucheira*.

2. *The dark marginal area or spots.*

In nearly all our common *Pierinæ* we find a dark patch at the apex of the forewing; better marked, as a rule, in the females than in the males. In *G. brassicæ*

it is large and crescent-shaped, extending for some distance along both costa and outer margin of the wing. In *G. rapæ* ♀ it is not as a rule prolonged very far on the outer margin, but it still reaches some way along the costa. In the male of the same insect it is generally small, and confined to the actual region of the tip. In neither of these species is there much indication of resolution, except that in most specimens of *G. brassicæ*, especially in the females, the hinder arm of the dark crescent shows an irregularity due to the massing of black scales about the marginal terminations of the nervules. But in *G. napi* (Fig. 16) resolution is generally well marked; and it becomes evident that the dark crescentic or triangular area of the tip is really formed by the fusion of the anterior members of the series S, which we have just been considering, with another series, which may be called M, occupying the actual margin of the wing, and consisting, in its fully resolved condition, of a row of dark spots, each of which is traversed by the peripheral portion of one of the nervules. It is noticeable that in this species the black marginal spots are often found extended, especially in the female, in the form of a powdering of dark scales along the course of the nervules towards the base of the wing.

Turning to *S. daplidice* (Fig. 15), we find the constituent elements of the apical patch still better shown than in *G. napi*. The marginal and submarginal series are always distinct, being separated from one another by portions of the general white colour of the wing, which take the form of a row of white spots on the dark apex, usually four in number. Either of these two species serves well to illustrate an important difference between the spots of the two series, S and M. The spots of the former series occupy, as we have seen, the interspaces between nervules; and when fusion between adjacent members of the series takes place, it does so by an extension of dark scales across a nervule. On the other hand, each of the spots of the latter series is centred, not in an interspace, but around the peripheral portion of a nervule or nervure. Thus the spots of the two series tend to alternate with one another, though this effect is to some extent interfered with by the frequent fusion of some of the spots with others of the same

series. It is further noticeable that in both of these insects the marginal series M is usually continued in the form of a row of dots smaller than those helping to constitute the apical patch, but still distinct, along the outer border of both fore and hindwing. In *S. daplidice* ♀ (Fig. 15), the submarginal series being also distinctly present on the hindwing, the alternate arrangement of the two series is in this situation very apparent. The constituent spots of series M may be numbered for convenience, in the forewing 1—11, in the hindwing 12—20, one being counted for each nervure or nervule that reaches the margin; and the same allowance may be made as was suggested in the case of S for the occasional suppression of a fourth or addition of a fifth subcostal nervule (see p. 255).

Many examples of the occurrence of this marginal series can be found among the near allies of the species just named, and in all of them there is a tendency towards the formation of a dark apical patch by the union near the tip of the forewing with the anterior members of the submarginal group S. In *G. gliciria* many members of the series are usually present, often tending in the females to form by fusion a broad marginal band in both fore and hindwing. Other species of the genus *Synchloe* besides *S. daplidice* present M in a fairly well-developed condition. It is usually conspicuous in the female *S. callidice*, *S. protodice* and *S. hellica*, and to a less extent in the males of the same insects; where it clings longest, as in the common species of *Ganoris*, to the region of the tip. *Tatochila autodice* and *T. theodice* show M in very nearly the same condition as the species of *Synchloe* last named.

Turning to the genus *Colias*, we find that the marginal series has undergone some modification. In the males it is often completely fused with the submarginal series, the two together forming a broad outer band to the wing, as in *C. edusa* ♂. The same may also take place in the female, as in *C. palæno;* but in most cases the two series, S and M, are in the female more or less distinct, being marked off from one another by areas of ground colour which take the form of a row of light-coloured spots, not unlike those present in many species of *Synchloe* (see p. 263). In some instances, as in *C. hyale* and *C. phicomone*, this description applies also

to the males. Most species show a strong tendency for the spots S 8 and M 8—9, and, in a less degree, S 10 and M 10—11, to become fused with one another by the obliteration of the separating patches of pale ground colour. The individual members of series M are usually more distinct from one another on the hind than on the forewing. Not infrequently they are fused into a complete band in both. On the lower surface M is in this genus rarely if ever visible; thus offering a strong contrast to S.

In *Meganostoma* the fusion of M with S is usually complete on the forewing; the females, however, of some species show traces of a separation; a few patches of the yellow ground-colour, like those in the females of many species of *Colias*, appearing in the midst of the dark border. In some forms, as *M. philippa* ♀, these light patches become much enlarged, and the two series S and M are as distinct from one another as in any species of *Colias*. *M. cesonia* usually shows the spots well on the upper surface of the hindwing; and in most species of this genus, M is often visible beneath as a row of minute pinkish dots on the terminations of the nervules at the margin.

In *Gonepteryx*, *Rhodocera*, *Amynthia*, and *Dercas*, the series is not as a rule strongly developed. *G. rhamni* usually shows on both surfaces a row of marginal dots, dark red or brown above and pinker beneath, at the outer extremities of the nervules, which are undoubtedly relics of M. These are best marked at the tip of the forewing, where they often tend to run into a thin continuous marginal line, and are generally more apparent in the female. The apical band is more strongly accentuated in *Rhodocera leachiana*, especially in the female, in which sex also M is often found on the hindwing in a fairly developed condition. Traces only of the series are visible in the species of *Amynthia*; but in *Dercas* M is reinforced by the anterior portion of S, and helps with it to form a conspicuous dark area at the region of the tip.

The condition of M in *Hebomoia* needs no special remark, except that on the under surface its separate existence appears to be sacrificed to the exigencies of the protective pattern.

In *Callidryas*, *Metura*, *Phœbis*, *Aphrissa*, and *Catop-*

silia, the development of M varies. Most of the species, however, show the usual tendency of M to expand into an apical patch, either with or without reinforcement from S. The members of the series are generally reduced on the lower surface of the hindwing to a row of marginal dots; and the great characteristic of the present series, namely that it belongs to the nervules, and not, like the former one, to the interspaces, is kept up throughout. On the upper surface of *Catopsilia flava* ♀ (Fig. 21), M and S are both well developed, and their relation to one another closely resembles that which obtains in *Colias*.

The same series is often present in the genera *Ixias* and *Teracolus*; being, as usual, most constant in the females, and most prominent on the upper surface. It appears occasionally as a chain of spots, as in the hindwing of many specimens of *T. ione* ♀, and some of *T. regina*, but more often as a simple marginal band, as in *I. marianne* (Fig. 18). This band may be completely fused with S, as in the hindwing of *T. phisadia*, or partially so, as in *T. amata*. A plain marginal band, in the forewing expanding at the tip and more or less indented opposite the branching of the median nervure, in the hindwing sometimes breaking into a chain of spots, is also the usual condition of M in the genus *Terias*.

In *Nepheronia* and *Eronia* M is generally present as a well-developed marginal band sometimes more or less fused with S, and often sending dark prolongations inwards along the course of the nervules. In some species, however, as *N. thalassina* and *E. leda*, it is mostly confined to the apical region; in the latter indeed it is absent from the hindwing of the male altogether, and barely visible on that of the female (Fig. 23). The series in *Euchloe* is generally recognizable as a row of dots, sometimes fused at the apex with the anterior members of S; but often, as in *E. tagis* and *E. ausonia*, preserving its independent existence.

The condition of M in the genera *Metaporia* and *Huphina* recalls that in *Nepheronia*; the constituent spots being generally fused into a marginal band from which dark offshoots run inwards, accompanying the course of the nervules. A similar description will apply to *Pontia*, though in this genus the dark markings are often greatly

reduced. *P. soracta*, however, shows M with sufficient distinctness; and even in *P. cratægi* M itself is in some instances visible, while the dark prolongations along the course of the nervules is a well-known and conspicuous feature.

Delias and *Prioneris* help to show us what is in all probability the earliest condition of the present as well as of the former series. The upper surface of both fore and hindwing in the female of *D. eucharis* presents once more the familiar pattern of *Metaporia agathon* and *Nepheronia gæa* ♀. It has already been pointed out that there is an easy passage from this system of marking to that which we find in *D. belladonna*, *D. pasithoe*, and several other species; while the same features are undoubtedly visible with but slight modification in the American genera *Euterpe*, *Catasticta*, *Leodonta*, and *Eucheira* (see p. 258). A comparison of the insects just named, to which may be added *Prioneris thestylis* and other species of the same genus, can hardly fail to suggest the probability of the origin of both M and S as portions of the original dark ground-colour marked off from one another with gradually increasing distinctness by the appearance, enlargement, and confluence of whitish patches in the interspaces between nervules. The alternate character of the two series S and M, when broken up into spots, is seen to be a consequence of the shape and position of the original dusky white touches that first bring them into view. These touches may be seen for example in *D. belladonna* (Fig. 4) to be divisible into two sets, which we may call marginal and basal, both occupying the central areas of the interspaces. Between the two sets is included the portion of ground colour corresponding to S, the constituent spots of which, when isolated, will necessarily have their centres in the interspaces. But the marginal set of light marks tends to reach by tapering extremities to the edge of the wing (see Fig. 5); so that the interposed marginal patches of unaltered ground colour, forming the first beginnings of M, are of necessity focussed round points in the nervules and not in the interspaces. And when in consequence of the further development and fusion of the white or pale markings, the marginal relics of dark ground colour become reduced to a row of isolated dark spots, these spots are, as we have already seen in *S. daplidice* (p. 263)

and other cases, always traversed by the peripheral portion of a nervule or nervure. This fact is well exemplified by *M. agathina, M. poppea,* and several other species of *Mylothris* (Fig. 12).

The invasion of white, which is already considerable in *D. eucharis* ♀, becomes still more predominant in the male of the same insect, where, however, the original ground-colour still persists, not only in the series S and M, but also in the form of the dark streaks accompanying the nervures and nervules, a feature which we have seen to be common in many other genera, especially *Pontia, Huphina, Metaporia,* and *Nepheronia.*

Without leaving the genus *Delias* we can find several examples where the intrusive white has ousted the whole of the original ground-colour, except at the margins and apex. This is the case for instance in *D. descombesii* ♂, *D. agostina* ♂, *D. cœneus* ♂, and *D. momea.* In most of these species the dark marginal area is plainly composed of S and M in a more or less complete state of fusion, and it is noticeable here as elsewhere that the female almost invariably retains a larger proportion of the original ground-colour than the male.

Many species of *Belenois* resemble the last mentioned species of *Delias* in the tendency towards fusion of the marginal and submarginal series. *B. peristhene* (Fig. 14) is exceedingly like *D. momea* in this respect, and in *B. teutonia* ♀ and *B. coronea* the fusion is still more complete. But in very many species of *Belenois* and *Pinacopteryx,* S and M are plainly distinguishable from one another; and in some, as in *B. calypso* (as also in *Pinacopteryx capricornus*), the resolution of both into a row of dots is complete. The formation of a series of rings along the margin of the hindwing (as in *Synchloe callidice* ♀, *S. protodice* ♀, etc.), by the union of the horns of the crescents or chevrons belonging to series S with the spots of series M, is a noticeable feature on both surfaces of many specimens of *B. mesentina* ♂ (see Fig. 13); and the identity of the whole arrangement of the submarginal and marginal series in *Belenois* with that in *Synchloe* becomes perfectly evident on a comparison of *B. mesentina* with *S. johnstonii* or *S. hellica.*

In *Appias* the two series when present are not sharply marked off from one another. In some species, however, S has almost or quite disappeared, and M may persist

alone as a marginal band, showing more or less tendency towards resolution (*Appias lyncida* ♂, *A. celestina* ♂, etc.).

Summary.—The present, like the preceding series, is thus seen to be a relic of the original dark ground-colour. It is intercepted between the margin of the wing and a series of pale touches (best seen in certain species of *Delias* and *Catasticta*) that making their appearance in the submarginal region of the interspaces, more or less isolate, indent and divide up the dark marginal area. It may eventually disappear altogether (as in some specimens of *G. rapæ* ♂), but usually persists on the forewing, at least, in the region of the apex. When present, it shows great variation in the extent to which it is resolved into separate spots, and also in the amount of fusion it undergoes with the neighbouring series S. As a general rule it is, like the last-named series, more constantly present in the female sex, and more completely resolved in the male.

3. *The light series between* 1 *and* 2.

The region of pale ground-colour included between the two dark-coloured series S and M, becomes of necessity more sharply defined and circumscribed as the constituents of each dark series become fused together into bands instead of remaining as rows of spots. The tendency so often seen of the two dark series to become partially fused with one another, by the extension between them of dark lines following the course of the nervules, leads, when carried far enough, to the splitting up of the included pale area into a series of pale spots, which sometimes attain a very distinct and definite character, especially at the apex of the forewing. These pale spots have already been incidentally noticed during the discussion of the two series between which they lie; it will not be necessary to do more in this place than to suggest that, for the purpose of separate reference, the letter I should be taken to represent the whole series, the possible constituents being numbered 1—20, in correspondence with the dark spots of series S which bound them on the inner aspect. (See Figs. 1, 2, 5, 21, etc.)

4. *The discoidal spots.*

In none of our three common species of *Ganoris* does

there exist a true discoidal spot. The nearest approach is to be found in *G. napi,* where the disco-cellulars of the forewing, together with the other nervules, are in many specimens accompanied by a sprinkling of black scales; which in some instances are sufficiently numerous in this particular region to give almost the appearance of a black discoidal spot or patch. This may be best seen in specimens of *G. bryoniæ,* but dusky specimens of the ordinary *G. napi* will sometimes show the tendency almost equally well. The same tendency is carried a little further in *Tatochila autodice,* while *T. theodice* shows the corresponding marks in a condition of strong development, with a slight indication of a similar feature on the hindwing as well. Passing to the genus *Synchloe,* we find the discoidal spot invariably present, at least in the forewing; and in most species large and distinct, especially in the females. *S. daplidice* (Fig. 15) has the spot well developed on both surfaces; on the lower surface it is more or less shaded with green. The same is the case with the somewhat smaller discoidal spot in *S. callidice.* Another example of a large and conspicuous discoidal spot is furnished by *S. hellica.*

In *Colias,* a discoidal spot is nearly always present on each surface of both fore and hindwings. On the upper surface of the latter it is sometimes independently present and sometimes only shows through from beneath; but it is seldom absent altogether. The spot on the forewing is in this genus, as in *Synchloe,* usually dark brown or black. It may be ringed or pupilled with orange; in the former case the orange is of a deeper shade than the general ground-colour. Examples of this may be seen in *C. meadii, C. cunninghamii,* and others. In *C. fieldii* and *C. edusina* the discoidal spot in the forewing is unusually large; in no species of *Colias,* however, does it overpass the boundaries of the subcostal nervure in front and the third median nervule behind. It may be very small, as in *C. barbara;* or entirely absent, as in some specimens of *C. palæno* and *C. pelidne.* On the lower surface it is often centred with white or silver. On the upper surface of the hindwing, the spot when present is not dark, but varies in different species from the palest yellow to a full orange. It is distinguished from the general surface of the wing either by its different shade of yellow or orange (as in *C. hyale*)

or by its freedom from admixture with the darker scales that often give the hindwing in this genus a comparatively dusky appearance (as in some specimens of *C. edusa*). In many species a small companion is visible in the interspace between the second subcostal and discoidal nervure. On the under surface the discoidal spot is much more distinct. Its centre is silvery white, and it is usually encircled with a brown or orange ring, which in some species is sharply marked off both internally and externally by thin marginal lines of a darker colour. The companion reproduces the discoidal spot on a smaller scale. It always occupies an interspace, whereas the chief discoidal spot is situated upon the second disco-cellular nervule. (Fig. 20, D 4.)

No doubt is likely to arise as to the identity of the discoidal spot in *Synchloe* with that in *Colias* so far as the forewing is concerned. The chief difference between them is that in the former genus the spot is less sharply defined and less regular in outline; moreover in *Synchloe* it frequently reaches forward to the costa, and it may extend backward to the space between the first and second median nervule; whereas in *Colias*, as we have seen, it does not pass the limits set by the subcostal nervure and the third median nervule. But there can be no reasonable question that the spots are homologous in the two cases; and a comparison of the two genera further suggests the probability that in *Synchloe* we have an older, in *Colias* a newer and more specialised form of the marking. This conclusion accords with what has been already said about the marginal and submarginal series of markings, which in *Colias*, especially in the males, have departed somewhat further from the original type than in *Synchloe*; and it will be seen to receive further confirmation from what is to follow. With regard to the discoidal spot on the hindwing, although it is perhaps not at first sight clear that the markings in the two genera are really homologous, it is nevertheless quite possible, on an attentive examination of allied forms, to trace the steps by which the passage from one to the other is effected. In the hindwing of many species of *Synchloe* there is no indication of a discoidal spot at all; in others, however, a definite aggregation of black scales is visible about the disco-cellular nervules. In some species, such as *S. protodice* ♀,

the nervules, though surrounded with black scales, are themselves covered with white, or (on the underside) pale yellow scales; a light-coloured centre being thus provided for the dark discoidal patch. In the genus *Tatochila* this light-coloured centre acquires greater importance. On the under surface of *T. autodice* the white scales are seen not only covering the disco-cellular nervules, but also intruding some way upon the yellow of the general surface; in this species, however, the pale patch thus formed has no dark border. But there can be little doubt, on a comparison of *T. autodice* with *Colias palæno*, that the whitish area surrounding the second disco-cellular nervule in the one is homologous with the silvery patch in the corresponding region of the other; while the identity of the discoidal marks in *Tatochila* with those in *Synchloe*, and of the same marks in *C. palæno* with those in other species of *Colias*, is a matter of certainty. The brown ring surrounding the silvery pupil on the under surface of most species of *Colias* is indicated in *C. palæno*, where its general appearance points to the probability of its origin from the dark scales that have already been noticed as gathering about the region of the disco-cellular nervules in *Synchloe*. In *C. palæno* itself, however, the central pale patch (as in *Tatochila*) becomes far more prominent than the surrounding dark border. An examination of the discoidal spot on the underside of the hindwing in *Gonepteryx rhamni* ♀ and *Amynthia mærula* will disclose the same general arrangement of a pale area traversed by the second disco-cellular nervule, and surrounded by a ring of darker scales, that we have already seen to be characteristic of the spot in other genera. In these insects, however, as in *Rhodocera leachiana*, the spots, though clearly identical with those in *Colias*, are in a lower state of development and specialization. Turning again to the discoidal spots on the forewing, we may at first sight hesitate to identify the bright orange spots in *G. rhamni* or *G. cleopatra* with the black spots or patches in *Synchloe* and *Colias*. But in *Amynthia clorinde* we have what is unmistakably an intermediate form of the spot, in which the vivid orange of the one closely encircles the deep brown or black of the other, and from which either the *Gonepteryx* or *Colias* type of spot might be easily derived. Much the same is the case with *R. leachiana*;

but in this insect the black markedly predominates. The discoidal spot in the forewing of *R. leachiana* is also noticeable as having a small companion, of similar character but with a greater proportion of orange, in the root of the interspace between the subcostal and the first discoidal nervure.

The discoidal spots in *Dercas*, when present, correspond closely with those in the genera just named. The spot on the forewing of *D. lycorias* is like that in *G. rhamni*; it is, however, less compact, and surrounds both disco-cellular nervules instead of the second only, as in the latter insect. The spot on the upper surface of the hindwing is scarcely visible, but those on both wings beneath nearly resemble the corresponding marks in *R. leachiana.* On the underside of *D. wallichii* the marks are of the same character, but reduced in size; from the upper surface they are almost or quite absent.

In *Meganostoma* the discoidal spots, both above and beneath, so closely correspond with those in *Colias* as to call for no special remark. In *Callidryas, Metura, Phœbis, Aphrissa,* and *Catopsilia,* they present also the same general appearance. On the upper surface of the hindwing, the discoidal spot is seen as a rule faintly or not at all; but on the forewing there is often a well-marked dark patch, enclosing either the second disco-cellular, as usually in *Catopsilia thauruma* and *C. catilla* ♀, or both disco-cellulars, as in *Aphrissa godartiana* ♀. On the underside the form of a silvery circular patch, surrounded by a pinkish or brownish ring, is almost universally kept up. There is in some species (as in *Callidryas philea*) a tendency for the discoidal spot in the forewing to divide into two parts, one for each disco-cellular nervule; while in the hindwing the small companion which has been already noticed in *Colias* is nearly always present in the interspace between the discoidal and subcostal nervures. One or two species (as *C. florella* ♀) possess a second companion within the cell. The present series, when fully resolved, seems thus to consist of five spots, two belonging to the two disco-cellular nervules in the forewing, the third belonging to the interspace between the subcostal and discoidal nervures in the hindwing, the fourth to the second disco-cellular nervule, and the fifth to the discoidal cell,

also in the hindwing. I propose to designate the system as D 1—5.*

The last-named genera exhibit a good deal of variation in the size of the constituent spots of D, and also in the breadth of the encircling darker ring. In *C. catilla* ♀, the latter, spreading widely out from the silver centres, and being reinforced in the hindwing by a similar development from certain of the spots of series S, forms a conspicuous dark red patch on the under surface of both primaries and secondaries. A similar tendency is seen in many specimens of *Callidryas thalestris* and other members of that genus. In all these cases the border of the discoidal spots on the under surface is assimilated in colour to the general character of the darker mottlings that form the prevailing feature of the wing-pattern. It is interesting to observe, in the case of *Phœbis trite,* that the straight diagonal streak already referred to (p. 260) as crossing the under surface of the hindwing is made up of elements belonging to both series S and D, as follows: The part between the two subcostal nervules is S 14; that between the subcostal and discoidal is D 3; the next, where the streak intersects the second disco-cellular, is D 4; it then skips a space, and reappears between the median and submedian nervures as S 19. That the homology of the different parts of this line has been correctly stated will be evident from a comparison of *P. trite* with *C. eubule* and *C. thalestris,* in which species the elements of the streak are visible in a separate condition. It is in *P. trite* particularly worthy of note that in those interspaces where D 3 and 4 form part of the streak, the corresponding members of S, viz., S 15, 16, and 17 (which are not wanted for this purpose), are visible well to the outer side of the streak; whereas in the other interspaces there are no marks between the streak and the margin, the members of S having been, so to speak, used up for another purpose, and having thus caused an apparent interruption of the usual submarginal pattern. In the interspace between the first and second median

* This use of D is open to the objection that the same letter has also been used for an entirely different set of markings in the Nymphalidæ (see Trans. Ent. Soc. Lond., 1890, p. 91). But I do not think that this circumstance is likely to give rise to any practical difficulty.

nervules, S 18 appears as a submarginal spot of the usual kind. Now, inasmuch as no member of series D ever occupies this interspace, there is no material at hand for continuing the streak; and, carrying the eye up to the apex of the interspace, where the streak should cross, we find it, in fact, deficient at that place.* This may seem a small point, but it is of interest as illustrating the absence of anything that might be called violent or arbitrary in the evolution of these various patterns, in which, indeed, the closer the examination the more difficult it is to find anything effected *per saltum.*

In *Ixias* the condition is again much the same as in *Colias*; the discoidal spot of the forewing, however, is often united on the upper surface with a dark band running across the wing from the costa to the anal angle. A similar feature occurs in *Hebomoia glaucippe* (Fig. 19) and other species of the same genus. On the lower surface the discoidal spot varies considerably in size, and in a few cases (as sometimes in *I. marianne*) may be absent altogether. When it is large, as in other specimens of *I. marianne,* it is frequently centred with white. In the hindwing the series is absent from the upper surface, and represented below only by D 4, which may also be white-centred, or may exist as a simple black dot of varying size.

In *Teracolus,* D is usually well marked. In some species, such as *T. vesta, T. hewitsonii,* and *T. puellaris,* it occurs on the forewing as a conspicuous black patch covering both disco-cellular nervules, and usually merged anteriorly in a dark or dusky band which extends along the costal border. In other species, as *T. evanthe, T. ione, T. regina,* etc., it takes the form of a circumscribed black spot, sometimes minute or absent. On the lower surface, the scales on and surrounding the disco-cellular nervules are often whitish, thus giving D a pale centre. D in the hindwing, when present, is usually small; on the underside of some species, as *T. danae, T. evippe,* and *T. omphale,* it is centred or shaded with orange;—this tint belonging primarily to the disco-cellular nervules, and spreading more or less widely from them.

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* As above noted (p. 260), the corresponding streak in the *forewing* of *P. trite,* and the somewhat similar feature on both wings of *Dercas lycorias,* are entirely formed out of series S.

In *Terias* and *Sphænogona*, D is constantly absent from the upper surface, but is usually visible below, where it may appear as a small black dot or pair of dots in each wing (*T. lisa*), or as a group of more or less regular narrow-bordered rings (*T. hecabe* and *T. floricola*), or in various intermediate forms (*T. deva* and *S. gratiosa*). The transition from the condition of D in *Colias* to that in *Terias* is well indicated by *Xanthidia nicippe*, most specimens of which correspond pretty closely in the markings of the lower surface with the latter genus; while the upper surface of the forewing bears a discoidal spot much like that in some species of *Colias*. In the closely allied genus *Pyrisitia*, D has altogether disappeared (see *P. proterpia*).

The genus *Euchloe* shows the discoidal spot on the forewing in a well-marked condition (Fig. 24). It may exist as a distinct spot, as in *E. cardamines*, usually larger in the female; or as a more or less quadrangular patch reaching up to the costa, as in *E. lucilla*. On the underside it is often white-centred, as in *E. belemia* and others. On the hindwing, D is in many species of *Euchloe* not visible at all. In some, however, it appears as a small, at times very minute, patch of black scales surrounding the second disco-cellular nervule (some specimens of *E. genutia* and *E. cardamines*); in others, as *E. charlonia* and *E. lucilla*, it takes the form, on the under surface, of a pale circular patch, closely resembling D 4 of *Colias palæno* in the same situation.

D in *Belenois* is usually well marked on the forewing, as a rule enclosing both disco-cellulars, and often prolonged anteriorly to join the outer extremity of a dark costal band; this is especially the case in the female, and on the under surface in the male, as in *B. mesentina*, *B. teutonia*, *B. calypso*, etc. The spot is sometimes small and quite distinct, as in *B. creona*, D 1 being absent; sometimes, on the other hand, it is large and almost or quite merged in the general dark field of the outer portion of the wing, as in *B. coronea*. In the hindwing there may be no discoidal mark at all, as in *B. creona*; or all the nervures may be covered with dark scales (as generally on the under surface of *B. mesentina*), the disco-cellular nervules not being specially distinguished; or there may be a definite discoidal spot, composed of D 4, as in *B. mesentina* ♀, upper surface;

and in *B. calypso,* under surface of both sexes and upper surface of female.

In *Appias* and *Catophaga* a discoidal spot can scarcely be said to exist; but in *Hiposcritia* and *Pieris* various members of the series D are often well marked. *H. lalage* ♂ (Fig. 11) has a conspicuous discoidal spot on both surfaces of the forewing, formed by D 2; and on the under surface of the hindwing there appears a minute representative of D 4. In *H. pandione,* D 1 and 2 compose a large spot which joins the dark costal band; while on the under surface of the hindwing, D 4 is sometimes indicated by a paling of the first disco-cellular nervule and the immediately surrounding area. In *Pieris* the forewing often shows a conspicuous discoidal spot, formed by D 1 and 2 or by D 2 alone; the hindwing as a rule possessing only a small dark representative of D 4 on the under surface, which in *P. buniæ* merely touches the second disco-cellular, but in *P. pylotis* encloses it.

In *Pontia* and *Huphina* (Fig. 8), D in the forewing appears generally as a mere darkening of the wing in the region of the disco-cellular nervules, more pronounced than the darkening of other nervures which is common in these genera, but not forming a definite spot. In the hindwing it is much less distinguishable or even absent (*P. cratægi, P. soracta, H. phryne, H. timnatha,* etc.). In *Metaporia agathon* (Fig. 7) the same darkening of the disco-cellular area occurs, which in *M. phryxe* takes the form of a definite and conspicuous patch. A like condition is seen in *N. gæa,* and other species of *Nepheronia.*

The correspondence in pattern of the genera *Delias* and *Prioneris* with those just discussed, already referred to on p. 267, applies to the present as well as to other features in the marking. *Delias,* moreover, shows in many species that paling of the disco-cellular nervules themselves, and sometimes of the immediately surrounding area in the midst of the dark discoidal patch, which we have seen to occur in *Synchloe* and other genera, and which in *Colias, Ixias,* and their allies leads to remarkable modifications in the general appearance of the discoidal spots (see *Delias aganippe, D. descombesi, D. crithoe,* etc.). In *D. belisama* ♀, the nervules remain dark, though there is a surrounding pale area.

Nothing special needs to be said about the genera *Euterpe, Catasticta, Leodonta,* and *Eucheira.* Their

general correspondence in pattern with the old-world genera last named, which has been already referred to, involves a similar condition of the present series D. In none of them does any member of D assume the condition of a definite circumscribed spot; but in nearly all, the series exists as a portion of the original dark ground colour between the touches of intrusive white or yellow. In *C. toca,* D on the underside of the hindwing consists of an irregular dark ring with a yellow centre traversed by the disco-cellular nervules, this representing an early condition of the homologous ocellus in *Colias.*

Summary.—This series also, like those already treated of, represents a local survival of the original dark ground-colour. Appearing in the first place as an ill-defined accumulation of dark scales around the disco-cellular nervules, it takes the form of definite spots as the invasion of white or other pale ground tint progresses. As in the case of the other series, resolution is generally best marked in the males; the females showing a greater tendency to adhere to the ancestral condition. When fully resolved, the series consists of five spots, two for the disco-cellular nervules in the forewing, and one for the second disco-cellular in the hindwing, with two extra spots, also in the hindwing. In many instances the disco-cellular nervules, with a varying amount of neighbouring ground-substance, may appear as pale streaks or patches in the midst of the primitive agglomeration of dark scales; and in the further development of the pattern it may happen that either the pale or the dark markings alone persist; or both may be retained and worked up as in species of *Colias, Callidryas, Ixias,* etc., into a system of more or less elaborate ocelli.

5. *The markings on the underside of the hindwing.*

a. The yellow precostal streak.—A constant feature in our common species of whites is a deep yellow or orange streak which occupies the margin of the precostal space on the underside of the hindwing, and is clearly distinguishable from the pale yellow of the general ground-colour. This yellow precostal streak is conspicuous in other species of *Ganoris,* as *G. gliciria,* and may also be seen in *S. daplidice, S. hellica,* and many other members of the genus *Synchloe.* It is, I believe, never found in *Pontia cratægi*; in the closely allied *P. hippia* and *P.*

soracta, however, it is well marked. *Metaporia agathon* and *M. phryxe,* which resemble the last-named species in other respects, also show a deep yellow mark in the same situation; but in this instance it occurs only as a spot bounded outwardly by the precostal nervure, and is not prolonged as a streak along the costa.* Many genera present this mark in much the same condition as the species of *Ganoris* first referred to; of which good examples may be seen in *Nepheronia thalassina, N. argia,* the curious *Herpœnia eriphia, Pinacopteryx pigea* and *P. capricornus, Mylothris chloris* and *M. agathina* (deep orange in these), *Tatochila theodice, Glutophrissa margarita, Appias zelmira, Phrissura sylvia, Daptonura lycimnia, Teracolus ione, T. regina, T. eris,* etc.

Looking back to *Synchloe hellica,* we find that the yellow precostal streak forms in that insect only one of a series of yellow marks, one or two of which partially occupy each interspace. A similar condition obtains in many species of *Belenois*; see for instance *B. mesentina* and *B. teutonia.* On the underside of the hindwing in these species, the dark lines following the course of the nervures, and the dark markings belonging to the various series above described, are laid down upon a ground colour which is usually white or pale yellow, but which in many specimens is relieved here and there by streaks and touches of a deeper yellow or orange. One of these streaks occupies the costa, and is plainly identical with the yellow precostal streak in *Synchloe, Ganoris,* and the other genera named. Although in the species of *Belenois* just referred to, as in several others, this streak is easily seen to form but one member of a series, it is nevertheless more constant and persistent than any of its companions. This is evident in those not uncommon specimens of *B. mesentina*† in which the general ground colour on the underside of the hindwing takes on so deep a yellow tinge as to approach that of the yellow streaks and touches. In these cases all or some of the latter set of markings may cease to be separately recognizable; the precostal streak, however, is always the last to disappear. In certain species of the

* A specimen of *M. agathon* in Coll. Brit. Mus. has, however, a few orange scales in the *outer* division of the precostal space.

† *I.e.*, the form known as *B. auriginea.*

present genus, as *B. gidica*, the ground colour remains pale; but the precostal streak is the only member of its series present. In others again, as *B. coronea*, the black spots of S exist in a state of enlargement and fusion, while the orange touches occupy nearly the whole of the spaces that are left. The light spots of series I (see p. 269) between S and M, which in *B. teutonia* are only touched with orange, are entirely of that colour in most specimens of *B. coronea*. In *B. peristhene* the amount of light ground colour is smaller still, but the orange costal streak and orange series I are present as in *B. coronea*. Both of these insects, *B. peristhene* in especial, suggest at once a comparison with certain members of the genus *Delias*, particularly *D. nysa* and *D. momea*. In these two species the yellow precostal streak and the yellow or orange series I are unmistakably present. In *D. nysa*, as in *B. peristhene*, these constitute the only relief to the general dark colour of the wing; while in *D. momea* S is partially defined by the presence of pale touches on its inner aspect in addition to the spots of series I along its outer margin.

While the species named suggest a passage in respect of this pattern of the underside of the hindwing between *Belenois* and *Delias*, there is not wanting evidence of the same import in the case of other species in which the blackening of the hindwing is a less conspicuous feature. On the underside of *D. belladonna* we cannot fail to recognize the counterpart of such a hindwing as that of *B. teutonia*; the dark and light areas occupy with slight modification the same relative positions, and the same spaces of pale ground-colour that are in *B. teutonia* touched up with deep yellow, are wholly or partially of the like colour in *D. belladonna*; among these, of course, being the precostal margin. The basal portion of the hindwing in such species as *D. eucharis* and *D. hyparete* shows a more general yellow tinge than in *D. belladonna*; but in both of these, as in other allied species, the deeper-coloured precostal streak is perfectly recognizable. In very many species of *Delias* we meet with a new feature, much of the ordinary yellow being displaced by a brilliant red; but the former colour still displays a tendency to cling to the region of the precostal space, as may be seen in *D. thisbe*; where, however, the precostal yellow hardly reaches further outwards than the pre-

costal nervure. In the very similar *D. pasithoe* it has been driven even from this position.

Prioneris exhibits a condition very similar to that of *Delias*. The underside of *P. thestylis* closely corresponds with that of *D. belladonna*, and the resemblance applies to the precostal streak no less than to other features. In some species of *Prioneris*, as *C. clemanthe* and *P. autothisbe*, the precostal yellow is again approached, and sometimes dislodged, by a greater or less amount of bright red, as in *D. pasithoe*, *D. thisbe*, *D. crithoe*, and other members of the former genus.

Leaving the red patches and other features of the pattern of this region in *Delias* and *Prioneris* for discussion at a later stage, we may pass on to the American genera *Euterpe*, *Pereute*, *Leodonta*, and *Catasticta*. In the two last-named the arrangement of light and dark markings corresponds generally with that in *Delias* and *Belenois*, and similar touches of deep yellow are mostly present in the same relative positions. One of these, usually to be seen on the costal margin, is clearly homologous with the precostal streak in the insects already referred to; in many specimens of *C. nimbice*, *C. semiramis*, *C. toca*, and others, it bears very much the same appearance as in the old-world genera above mentioned. It may be noticed in passing that in many instances, such as *L. zenobia*, *L. dysoni*, and *C. anaitis*, the yellow precostal streak is found sharing the precostal space with a greater or smaller amount of brilliant red, as we have seen to be often the case in *Delias* and *Prioneris*. The same struggle between yellow and red is visible in the genera *Euterpe* and *Pereute*. In *E. tereus* the space is shared, the red keeping to the inner, and the yellow, when present, to the outer side of the precostal nervure. In *P. charops* the space is usually all yellow; in *P. autodice* and *P. leucodrosime* it is all red. In these two genera the other yellow marks are reduced in number or completely abolished; *P. charops*, however, generally has a conspicuous yellow patch between the costal and subcostal nervures which undoubtedly belongs to the series.

In the genus *Pieris*, which is also American, some species, such as *P. locusta* and *P. habra*, show on the under surface of the hindwing a pattern which is evidently only slightly modified from that seen in many

species of *Catasticta;* and in these also the red or orange of the costa is a prominent feature. In other species of *Pieris* a farther alteration has taken place, and the markings have been swept from the basal portion of the wing (as in *P. demophile*), or away altogether (*P. buniæ*). In most, however, if not all of these cases, the precostal streak persists, again taking a yellow rather than red or orange colour; and, in the absence of other yellow or well-defined dark marks on the wing, it comes to resemble very closely the corresponding feature in so many species of *Synchloe* and *Ganoris*.

Summary.—The facts adduced in the course of the foregoing remarks seem so far to allow of little doubt as to the history of the yellow precostal streak. It is evidently a survival of a series of yellow or orange marks which is found, in many genera of both eastern and western Pierinæ, on the underside of the hindwing, partially or wholly occupying the paler areas left between the relics of the original dark ground colour. The greater number of these marks may disappear with a general lightening of the wing, or the whole wing may become so yellow as to render them almost or quite indistinguishable; but the particular yellow streak that occupies the margin of the precostal space is more persistent than any of the others, and may remain, as in our common species of *Ganoris*, after every other characteristic of the ancestral marking has departed. It will be seen later that this account of the precostal streak, though no doubt correct as far as it goes, in all probability needs supplementing.

b. The red basal patch.—In both British species of *Colias*, there occurs at the base of the hindwing, on the under-surface, a pinkish patch, which occupying the apices of the cell and of the median and submedian interspace, and also in most cases a small area at the root of the precostal space, is often prolonged for a short distance along the middle of the cell. This patch, which is almost always present throughout the genus *Colias*, is found in most if not all species of *Meganostoma*, and also very commonly in *Catopsilia*, *Callidryas*, *Phœbis*, *Aphrissa*, and *Metura*. It is present, too, in *Dercas*, *Gonepteryx*, *Rhodocera*, and *Amynthia;* in these, however, it does not as a rule extend far from the body itself. Beyond the limits of these closely-allied genera this

special feature does not often occur in a very clearly-marked condition; it is, however, present in *Xanthidia nicippe*, and in several species of *Terias* and *Sphœnogona*, as *T. agave* and *S. mexicana;* it may also be seen occasionally in *Teracolus*, as in *T. antevippe*, *T. eupompe*, and (sometimes) *T. eris*, assuming in this genus a somewhat diffuse appearance. In some species of *Appias*, as *A. hombronii* (occasionally), and *A. lyncida*, as also in *Herpænia eriphia*, there are deep yellow marks near the root of the wing, which are probably homologous with part of the patch now under discussion; and in the genera *Belenois* and *Tatochila* touches of deep yellow often occur at the base of the median space, though not in the cell, which appear to correspond with the marks just referred to in *Appias* and *Herpænia* (see *B. mesentina* and *T. autodice*). These yellow touches in *Belenois* are undoubtedly members of the series spoken of on p. 279, and so far it would seem that the well-marked pink patch at the root of the cell in *Colias*, *Gonepteryx*, etc., is at least in part developed from a portion of that series, of which another member has given rise to the yellow precostal streak. It is certain, however, that other factors besides the series now indicated are chiefly, though probably not entirely, answerable for the composition of the pink basal patch in *Colias;* and it is at least possible, as will presently be seen, that the precostal streak itself owes something to their assistance. These other factors are the red basal areas to which reference has already been made, and which will now be examined in greater detail.

c. *The red basal areas.* To begin with the underside of *Delias pasithoe*, we find the base of the hindwings occupied by a bright red patch forming about a quarter of a circle on each wing, the body itself and the immediately surrounding area of the wings being black. The spaces affected by the red patch are six; namely, the precostal, costal, subcostal (or cell), median, submedian, and internal—all those in fact whose apices reach to the base of the wing. In *D. thisbe* there occurs a similar red patch, occupying nearly the same spaces. In this insect, however, there is no red in the precostal space, which is occupied (as above noticed, p. 280) by the ordinary yellow precostal streak; while the red patch, which in this butterfly is visible on the upper as well as the underside

of the wing, includes the apex of the space between the first and second subcostal nervules in addition to those above enumerated. *D. egialea* shows the same condition as *D. pasithoe*; but in *D. crithoe*, otherwise similar, the precostal space is black. In *D. descombesi* and *D. belisama* the red is confined to the costal interspace (*i.e.* the space between the costal and subcostal nervures); while in *D. cœneus* a submarginal set of roughly-defined red spots or dashes continues round to the anal angle the series begun by a red mark in the costal interspace, corresponding with that in the two preceding species. The submarginal series which, so to speak, becomes infected by the red coloration, is undoubtedly that spoken of above as series I (see p. 269). This latter feature of the Pierid pattern, somewhat indefinite in *D. cœneus*, becomes much more distinct in such species as *D. nigrina*, *D. harpalyce*, *D. aganippe*, *D. eucharis*, and *D. argenthona*. The latter of these has another well-marked red spot surrounding the second disco-cellular nervule, which represents a diffused reddish area in *D. duris*, and a more circumscribed patch in the same situation in *D. cœneus*. In *D. hyparete* S is going from the underside of the hindwing; in *D. hierte* it is gone; but in both cases the red spots of I remain in their full development. *D. mysis*, *D. isse*, *D. echo*, and other species exhibit the same feature in a more or less conspicuous manner.

The same red coloration is visible, as we have seen, on the underside of many species of *Prioneris* in the form of a basal patch; and in one species (*P. sita*) it spreads to the submarginal spots of series I, exactly as in *D. eucharis*. In *P. autothisbe* the red is found in the costal and subcostal interspaces; in *P. clemanthe* and *P. vollenhovii* only in the inner division of the precostal space, whence it spreads inwards upon the body.

In the American genera *Euterpe*, *Pereute*, *Leodonta*, and *Catasticta*, the red is usually present; but as in *Prioneris* and the *pasithoe* group of *Delias*, it is mostly confined to the basal portion of the wing.* In *E.*

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* An exception to this rule is furnished by *Euterpe tereas* and *E. critias*, in which species the area of light ground colour immediately internal to that region of the wing which corresponds to the submarginal series S, is on both surfaces more or less deeply tinged with the same red colour as that of the basal patches. This feature is due to mimicry, the two species named

tereas, E. critias, C. bithys, and *C. anaitis,* it most commonly occurs in the inner division of the precostal and the internal space; in *Leodonta zenobia* and *L. dysoni,* in the precostal and costal. In *L. tellane,* besides the bright red patches of the precostal and costal spaces, scales of the same colour occur in the apices of the subcostal, submedian, and internal spaces—of all, in fact, except the median. *Pereute leucodrosime* has the precostal and costal red patches; so also has *P. swainsonii*; but in *P. charops* these spaces are occupied by yellow streaks with no accompaniment of red.

Even in the genus *Dismorphia,* profoundly altered as it has been by mimicry, the same marks occur. *D. melia* has a conspicuous red spot in the inner division of the precostal space; while *D. astyocha, D. praxinoe,* and others possess a very clear representative of the same spot, with another one in the median interspace. The colour in these latter species is seldom so bright as in the first-named; it displays, in fact, a tendency to become assimilated to the chestnut tinge of other portions of the wing; the spots are nevertheless quite recognizable, and undoubtedly correspond with those in the former genera. In some species, such as *D. nemesis,* there is no red, but an indication of the yellow precostal streak is plainly visible.

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offering a very close resemblance to the females of *Papilio polymetus* and some of its allies, in bringing about which resemblance the red areas of the hindwing take a considerable share. It is interesting to observe that good as is the general effect of the imitation by these Pierines of the *Papilio* pattern, the imitative process has its limitations, and is seen on a strict examination to fail in more than one particular. Thus, (1) the Pierine is able to produce an excellent representation of the Papilionine reds and yellows, but apparently it never reproduces the metallic blues and greens, of which touches are found in the males of several of the mimicked species; (2) the costal and submedian spaces in the Pierine invariably retain their yellow patches on the underside; these are never yellow in the *Papilio*; (3) the red basal patches on the underside of the Pierine give just the same general effect as similar patches on the *Papilio*; but a close scrutiny will reveal the curious fact that the patches of the Pierine belong always to the wing, and those of the *Papilio,* in almost every instance, to the body. The wide distribution of the red basal patches among the *Pierinæ* forbids us to suppose that they were evolved for the purpose of mimicry in these few species; but it is worth noting that their presence affords material ready to hand for a sufficiently deceptive though not absolutely exact copy of a conspicuous Papilionine feature. See also note on p. 298.

In those species of *Pieris* (such as *P. habra* and *P. locusta*) which present on the underside of the hindwing a pattern only slightly modified from that of *Leodonta* and *Catasticta*, the red basal marks are clearly to be distinguished. A bright red patch characterises the inner division of the precostal space, and in most specimens is also prolonged into the outer division, while the apices of the median and internal spaces are likewise provided with conspicuous red touches. Comparing the underside of *P. locusta* with that of any of the American mimetic forms of *Mylothris*, we cannot well resist the conclusion that the central horizontal red or chestnut band in the latter species represents the touches of red in the median and internal spaces of *P. locusta*. The relation is best traced in the case of *M. lypera*, in which insect the part played by the yellow streak of the costal interspace in the production of the mimetic pattern is also clearly to be seen; but other species, such as *M. lorena* and *M. pyrrha*, whose mimicry of Heliconine forms is further advanced than that of *M. lypera*, still show the origin of the central red band almost equally well. In *Hesperocharis hirlanda* a somewhat similar effect is produced by slightly different means. The basal red is here confined to the precostal and internal spaces, not being found (as in *Pieris*) in the median. The horizontal red band is therefore not central but costal, its innermost extremity being constituted not (as in *Mylothris*) by the red patch of the internal space, but by that of the inner division of the precostal. The whole of the precostal red, which is absent in the three species of *Mylothris* just referred to, is prominent in *H. hirlanda*. Although these differences involve a change in the relative position of the horizontal bands of red and pale yellow in the latter species, yet the general resemblance of the underside to that of *M. pyrrha* ♂ is considerable, and is probably quite enough to tell perceptibly in the insect's favour. Other species of *Hesperocharis*, which are unaffected by mimicry, show the basal marks in the same position, but, as a rule, not very definitely, except at or near the root of the precostal space. Here there generally occurs an orange spot which partly represents the red precostal patch in *H. hirlanda* (see *H. nereis*, *H. marchalii*, and *H. anguitia*), but which in some species (as

H. erota) can be distinctly seen to belong to the apex of the median interspace as well as to the root of the precostal.* A similiar orange spot is visible in several species of *Pieris*, such as *P. buniæ* and *P. thaloe*; and of *Leptophobia*, as *L. elodia* and *L. eleusis*. In the last-named insect again it can generally be made out that the orange spot does not belong entirely to the root of the precostal space, but is furnished with a constituent from the apex of the median interspace as well. This double character of the spot is much more evident in *L. tovaria*; and on referring once more to almost any species of *Colias*, the conviction forces itself strongly upon us that in these basal marks in *Leptophobia*, *Hesperocharis*, and *Pieris*, and so in *Euterpe*, *Leodonta*, *Catasticta*, and consequently even in *Delias* and *Prioneris*, we see represented the chief material out of which the pink basal patch in *Colias*, *Gonepteryx*, *Catopsilia*, and their allies is constructed. It is probable that, as above suggested, another element may enter into the composition of the basal patch in these genera, namely one or more members of the series of yellow streaks; a conclusion which seems to be somewhat favoured by the condition in *Belenois*, *Herpænia*, and *Appias*; but the two series are distinct enough from one another in such genera as *Catasticta* and *Leodonta*; and an unnamed species of *Hesperocharis* in the British Museum shows, still more plainly than those above mentioned, the co-existence of a relic of the basal red in the situation of the pink patch in *Colias*, with a series of yellow streaks in the interspaces like those of *Catasticta* and *Belenois*.

Summary.—With regard to the whole assemblage of red and yellow marks on the underside of the hind-wing, the following appear to be the most probable conclusions:—

The yellow precostal streak so commonly seen in butterflies of this group, including our common British species of *Ganoris*, as also the pinkish patch at the apex

* In order to avoid a possible ambiguity, I may here mention that I regard the "apices" of the interspaces as pointing towards the "base" of the wing. When a precostal nervule is present, I speak of an "outer" and "inner" division of the precostal space, the nervule forming the line of demarcation. By the "root" of the precostal space, I mean the part immediately adjoining the body.

of the cell, of which our native species of *Colias* and *Gonepteryx* present good instances, are relics of a more elaborate system of marking seen in a high condition of development in various exotic genera. This system consists essentially of a series of red and yellow markings occupying more or less completely the pale spaces included between the radially disposed dark lines that coincide with the nervures on the one hand, and the concentrically arranged dark spots or bars of the marginal and submarginal series on the other. That this system of markings is a very primitive one is rendered probable by the fact (1) that it is represented by vestiges in so many genera of both hemispheres; and (2) that it occurs in a well-developed condition in genera so widely separated in a geographical sense as the South American *Leodonta* and *Catasticta*, and the Australian and Indian *Delias* and *Prioneris*. As a general rule, the spaces at the base of the wing tend to be occupied with red, and those on the disc and at the periphery with yellow; but in some cases, as has been seen, the red may encroach upon the submarginal yellow (as in *Delias cœneus*, *D. eucharis*, *D. argenthona*, etc.), or may be prolonged from the base in various directions across the wing (*Hesperocharis hirlanda*, *M. lypera*, *M. pyrrha*, and other American species of *Mylothris*). In the first-named genera, which exhibit the system in its full state of development, the distinction between the red and yellow markings is a perfectly easy one; but in such genera as *Pieris*, *Leptophobia*, *Hesperocharis*, *Belenois*, *Ganoris*, *Synchloe*, and *Colias*, whose markings are no doubt ultimately derived from the *Catasticta* and *Delias* pattern, it is not always easy to say to which part of the original system the relics that are present belong. On an inspection of all the forms, it would, however, seem to be the case that those members of the yellow part of the system most often persist which are capable of being reinforced, as it were, by a neighbouring red patch towards the base of the wing. For instance, the most persistent marking of all is, as we have seen, the yellow precostal streak. This is in most species of *Leodonta* and *Catasticta* closely bordered on by a bright red spot in the inner division of the precostal space; and on tracing the condition of that space from these more ancestral genera downwards, through *Pieris*, *Leptophobia*, and

Hesperocharis, we find it become tolerably evident that the dark yellow vestige which at last alone remains is the result of a kind of convergence both in colour and position of the yellow and red markings that at first lie simply side by side and are clearly distinguishable the one from the other.* A further instance of possible convergence is supplied by the basal pinkish patch, found in the group of genera headed by *Colias,* which we have seen reason to identify with original markings of both the red and yellow kinds.† In other cases, the persistence of various members of the present system is determined by the exigencies of a mimetic pattern, as in the species of *Mylothris* and *Hesperocharis* above referred to (p. 286).

III. Phylogenetic Conclusions.

1. *The evidence of the Wing-markings.*

We are now in a position to consider as a whole the various sets of facts that have been above recounted, and to endeavour to construct, from the evidence at hand, a theory of the phylogenetic history of the entire group. This, of course, is only attempted under the

* This, it is true, applies only or mainly to the New World forms; the similar basal red patch that partly occupies the precostal space in certain species of *Delias* and *Prioneris* not seeming to have left any traces in those Old World genera (*Belenois* and *Teracolus*), which appear to stand in much the same relation to *Delias* and *Prioneris* as *Pieris* and *Hesperocharis* do to *Leodonta* and *Catasticta*. The deep orange, however, of the precostal streak in some Old World species of *Mylothris* (as *M. chloris* and *M. agathina*), and in some species of *Belenois* (as *B. helcida*) which resemble them, may perhaps be derived wholly or in part from the precostal red; but if so, it does not bear in itself a plain record of its origin as does the like feature in the corresponding genera from America.

† Again, in *Pieris pylotis* the only marking to be seen on the under surface of the hindwing (besides the basal spot) is a short and narrow orange streak near the apex of the median interspace—an interspace that in more primitive forms, such as *P. locusta*, *Mylothris lypera*, and others, is provided with an apical red patch. It is also worthy of notice that in many species of *Belenois* the spots of series I are apt to retain or assume an unusually deep yellow or orange colouring like that of the precostal streak—this series being in some species of *Delias*, and at least one of *Prioneris*, a sharer in the bright red of the basal patches (see p. 284).

limitations above referred to, and is not to be taken as more than a connected statement of the probable import of the facts derivable from one particular source—those facts, namely, which relate to the colours and markings. I need hardly say that I recognise to the full that any phylogenetic conclusions founded on these data must of necessity be open to checking and correction in the light of information arrived at in other ways.

The evidence that has now been examined seems to indicate that the wings in the earliest form of Pierine were uniformly overspread with a dark neutral tint.* The first variation from this condition appears to have occurred by the paling of certain areas in the principal interspaces between the nervures; a modification that may be seen in probably its simplest extant form in the remarkable American Pierine *Eucheira socialis* (Fig. 1). Here each interspace, including the discoidal cell in both wings, possesses a more or less definite pale patch, those of successive interspaces being so arranged as to form a somewhat indistinct and interrupted band crossing the disc of both wings from the costa to the inner margin. Besides this central series of pale patches, there is also a submarginal row of much smaller and fainter spots of the same greyish-white hue. The whole pattern is repeated with very little change on the under surface, but on the hindwing with even less distinctness than above. The underside of the hindwing in this insect, indeed, probably exhibits the very oldest kind of Pierine colouring to be seen in any existing species.†

The primitive system of marking manifested by *Eucheira socialis* persists with little alteration on the upper surface of many species of *Catasticta,* as, for

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* This accords generally with the opinion expressed by Mr. Wallace: "There are, in fact, many indications of a regular succession of tints in which colour development has occurred in the various groups of butterflies from an original grayish or brownish neutral tint."—"Darwinism," 2nd edition, 1889, p. 274.

† While entirely agreeing with Staudinger and Schatz that the remarkable forms *Styx infernalis* and *Pseudopontia paradoxa* are probably of great antiquity, I cannot but regard the special Pierine affinities claimed for them by these authors (and especially for the latter) as more than doubtful. See Staudinger, Schatz, and Röber, "Exotische Schmetterlinge," 1892, *sub voc.*

instance, *C. bithys* (Fig. 2), *C. toca*, and *C. colla*. In other species of the same genus, the next steps are shown by the enlargement of the pale spots (as in *C. anaitis* ♂), their assumption of a purer white colour (as in *C. anaitis* ♀), and the confluence of those of the inner row, as in *C. trœzene* and *C. ctemene* ♂. In the latter insect the enlargement and confluence of the white patches has proceeded so far that the white must now be considered the ground colour, the original dark neutral tint being confined to the base and apices of the forewings, a narrow and interrupted marginal band on the hind-wings, and the course of the nervures with their branches (Fig. 3). In *C. corcyra*, the same process is continued almost to its furthest limit, the new ground colour has supplanted the old in every place except the apex and a narrow slip along the costa of the forewing. *C. corcyra* is thus practically a "white" butterfly; and so within the single genus *Catasticta* a complete transition is to be found, from a dark almost black ground colour, with small and indistinct pale greyish patches, to a ground colour of dead white, with hardly more than a trace remaining of the original dark surface tint. This passage from *C. bithys* to *C. corcyra* is really an epitome of the whole range of variation in pattern throughout the entire group of *Pierinæ*.

In such species of *Catasticta* as *C. semiramis*, where the pale patches are tolerably distinct, and have not yet coalesced, the dark marginal and submarginal series of spots, so characteristic of the Pierines as a whole, are visible at an early stage of their emergence. As has been shown above, on p. 267, the marginal series (called M) is formed by the remains of the dark ground colour between the outer series of primitive pale patches and the outer border of the wing; while the sub-marginal series S comes into view between the outer and inner series of pale patches. Besides these, a relic of the dark ground colour is seen to remain about the disco-cellular nervules in the forewing, which forms the first beginning of a definite discoidal spot; and another row of minute pale patches, each occupying the centre of an interspace on the extreme outer margin of the wing, begins to split up the marginal series in the manner already spoken of. The definite character of series M is assumed sooner on the forewing than on the

hindwing, and in the latter situation the discoidal spot has at this stage scarcely become recognizable; in some species, however, a patch of pale-coloured scales covers the lower disco-cellular nervule of the hindwing in the midst of a wide and not sharply-defined area of dark ground colour.

So far little or no essential difference has been noted from the primitive pattern of *Eucheira socialis*; the variations produced having simply resulted from a greater or less extension of the intrusive pale tint along the lines originally marked out. But, on turning to the underside of any species of *Catasticta*, we find what at first sight appears to be a very considerable divergence. A careful examination, however, soon makes it plain that the pattern of the lower surface is throughout the genus essentially the same as that of the upper surface, though one or two new features are superadded. Confining our attention in the first place to the forewing, for instance in *C. nimbice*, we find the submarginal series S and the discoidal spot shown at least as clearly as on the upper side; while from the greater prominence of the pale spots at the extreme margin, M is brought still more plainly into view below than it is above. On the hindwing, the central pale band may be easily traced across the disc of the wing, leaving on the one side of it a basal, and on the other a broad marginal dark area. Traversing the latter can be seen a row of elongated, more or less wedge-shaped, yellow streaks, which represent the more easily recognized series I of the forewing; while a distinct row of yellow spots on the extreme margin continues the similar series from above. Though S and M are not yet sharply marked off from one another, the portions of dark ground colour to which they respectively belong are already separately recognizable. The undersides of *C. nimbice, C. colla, C. toca*, and *C. corcyra* will be found to make a very good transitional series, showing the gradual emergence of S and M and the subsequent reduction of each to a mere festooned line.* The superadded features above alluded

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* An unnamed species of *Catasticta* in the British Museum presents a condition of the underside of the hindwing more exactly intermediate between *C. corcyra* and the usual type than any of the species mentioned. An individual of the same species is in

to are (1) the streaks and touches of yellow that begin to occupy much of the area of the original pale patches, including, as has been seen, the spots of I on the hindwing; and (2) the bright red patches visible in the basal region of the same wing close to the body. These have been already discussed at some length (see pp. 281, 285), and their importance has been shown in reference to the markings of more recent groups. In this place it is only necessary to note once more that their ancestral character seems to be proved not merely by their existence in a fully developed condition in genera so widely separated geographically as the Western *Catasticta* and *Leodonta* and the Eastern *Prioneris* and *Delias*, but also by the fact that there is scarcely a genus throughout the whole sub-family, whether in the Old or New World, that does not show some relic of their former presence. With regard to their origin, no clue appears now to exist. It seems impossible to trace them further back than to the Eastern and Western genera named; and the probably still more primitive form, *Eucheira socialis*, to which we should naturally turn for an indication of their development, affords us in this particular no information whatever.

In the genus *Leodonta* we find some modification in the shape of the wings, and only three instead of four branches to the subcostal nervure of the primaries. But the wing pattern remains much the same as in those species of *Catasticta* where the white central band has grown into a well-defined area and the two series S and M have not yet become clearly distinguishable. The yellow streaks and red basal marks are still prominent on the hindwing beneath, and the separation between S and M is, in this genus also, more evident on the underside.

In *Pereute* and *Euterpe*, which are undoubtedly very close allies of the genera just referred to, the development of the pattern has taken a somewhat different direction. The primitive dark ground colour is in the males of several species of *Pereute*, as *P. charops*, *P. autodyca*, and

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the Hewitson collection labelled as *C. notha*. This is undoubtedly erroneous, as the underside of the true *C. notha* is almost exactly like that of *C. corcyra*.

P. swainsonii, relieved by dustings of pale pinkish or bluish grey, which do not seem to bear any particular relation to the lighter patches in *Catasticta* or *Eucheira*. These greyish areas are often, especially in the females (including those of the species named), brightened up into bars or broader expanses of vivid red (*P. leucodrosime*) or blue (*P. telthusa*), and the aspect thus produced is very unlike that of nearly all the members of the allied genera. But as has been shown above, at pp. 281 and 285, an indication of affinity in coloration with those genera is preserved in the red and yellow patches of the underside of the hindwing; and, what is very remarkable indeed, there are two species of *Catasticta*, namely *C. teutamis* and *C. ctemene*, the males of which are of the usual *Catasticta* type, while the females present, together with the ordinary *Catasticta* neuration and structure, the aspect characteristic of *P. charops* ♀ and other highly coloured members of the genus *Pereute*. In the case of these two *Catastictas* there can, I think, be no doubt that it is the male rather than the female that represents the ancestral colouring of the group, and we are thus led to the conclusion that some common cause has brought about the divergence in the same direction of these female *Catastictas* and both male and female *Pereutes* from the ordinary character of their nearest relatives. This cause I believe to be mimicry, the models for which in the present instance are to be found in certain species of *Heliconius*, particularly *H. melpomene*, *H. phyllis*, and their allies.* The resemblance is not perfect,† but in all probability is quite sufficient to be of much service to the Pierine mimics; and we find exemplified here, as in many other cases, the much greater readiness with which the female assumes the protective coloration. As we

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* I also think it exceedingly likely that *Papilio euterpinus*, Godm. & Salv. (Ecuador), forms one of this mimetic group. It is, however, remarkable that its range seems not to coincide with that of the Pierine, namely *P. charops* ♀, which probably resembles it most closely in size as well as colour.

† The red colour of the species of *Heliconius* here mentioned (to which may be added *H. vulcanus* and *H. hydara*), as they occur in collections, is by no means so vivid as that of their supposed imitators. But Mr. A. G. Butler and Mr. F. A. Heron both inform me that the red in *Heliconii* has a special tendency to lose its brightness, even in specimens carefully preserved in the dark.

have seen, the male *Catastictas* are not affected at all; while in most species of *Pereute* the males have not advanced nearly so far along the mimetic path as have the females. Another point worthy of observation, which is paralleled elsewhere, is the fact that the males show a much closer approach to the complete mimetic pattern on the lower than on the upper surface.*

A similar explanation will apply to the even more remarkable divergence shown by the genus *Euterpe*, though here the phenomena are so curious and complex as to require a more detailed treatment. This genus (as restricted by Butler, Cist. Entom. i., pp. 34, 42) does not contain a single form that reproduces in general aspect the typical Pierine features; every species indeed is the subject of a mimetic change, and such marks of their origin and relationships as they retain, are used up in a more or less modified condition to help in the production of the deceptive pattern. Thus we have seen how in *Euterpe critias, E. tereas, E. rosacea,* and allied species, the area representing the white central band on the hind-wing, now tinged with rosy pink, has become an important ingredient in the general imitation of *Papilio zacynthus* ♀; the red basal patches on the under surface also taking their part in the picture. There is, moreover, little doubt that the white spot on the forewings is identical in origin with the usual white central bar, while for the marginal yellow spots a counterpart is easily found in *Catasticta nimbice* and many of its allies. In *Euterpe bellona* we find the patch on the forewings bright yellow instead of white, while the rosy patch is intensified in colour and split up into three or four brilliant streaks radiating from the base towards the margin of the wing. The general effect is not very dissimilar from that of *E. critias,* and the identity of the markings is beyond question; nevertheless the changes, slight as they are, are highly significant, for they import nothing less than the substitution of a member of the Heliconine for one of the Papilionine group as a model for imitation. *Euterpe bellona* undoubtedly mimics the Heliconine group of which *H. thelxiope* and *H. burneyi* are conspicuous members; and it would be difficult to find a better instance to show how slight a

* See Weismann, "Studies," vol. i., pp. 7, 8 (English Edition).

modification of an existing pattern may suffice to produce an effective copy of an entirely different insect. Facts of this kind seem to go a long way towards answering such objections to the theory of mimicry as those alluded to by Mr. Beddard in his "Animal Coloration," 1892, pp. 214, 215.

It is very remarkable that red basal patches, like those of the mimicking Pierines, occur on the underside of the hindwing in most, if not all, of the Heliconii and Papilioninæ mimicked by members of the genera *Pereute* and *Euterpe*; and in some, *e.g.*, *H. melpomene*, there is even a well-defined yellow precostal streak. Now although there is no difficulty in ascribing most of the features in the coloration of these Pierine genera to the operation of mimicry, it would seem, for the reasons given above (p. 285, note), that the origin of these particular marks, which are so wide-spread and so persistent throughout the whole Pierine subfamily, must be excepted. Nor, in the absence of any evidence of a direct causal relation, does it seem to my mind more satisfactory to consider the occurrence of these patches in the three diverse groups, Papilionines, Heliconines, and Pierines, as the effect of similar external conditions. If we assert them to be purely "accidental," we are met by the fact that although they are found in some species of both *Papilio* and *Heliconius* that are apparently not the subject of mimicry, yet they are most distinct and most prevalent in those species that are copied by Pierine imitators; and the same considerations (amongst others) seem to show that the supposition that they are simply due to inheritance from a common ancestor of all the groups must be inadequate. Before the phenomenon is dismissed as inexplicable, it may be worth while to consider the following suggestion.

According to the well-known principle laid down by Fritz Müller and expanded by Meldola, by which these authors have been enabled to account for cases of parallel resemblance between the species of protected genera, and also of the grouping of allied inedible species into distinct sets, each with its own scheme of coloration,* it

* F. Müller in "Kosmos," 1879, p. 100; Meldola in "Proc. Ent. Soc. Lond.," 1879, p. xx., and "Ann. and Mag. Nat. Hist.," Dec., 1882. See also Wallace, "Darwinism," 2nd ed., 1889, pp. 249–257, and Poulton, "Colours of Animals," 1890, pp. 192–195.

is advantageous for any two or more protected species to join their forces, in order to share the toll levied upon them by inexperienced enemies. In such cases it no doubt often happens that one species serves as the standard to which the others conform, whether by way of convergence or of arrested divergence; but there seems no reason why, especially if there is no conspicuous inequality of numbers, there should not be a kind of "give and take" arrangement between mimicker and mimicked, the latter advancing some way to meet the former for their mutual benefit. In other words, when two species, A and B, form an association of this kind, it need not be supposed that the form of A remains fixed, while B assimilates itself to it, or *vice versa;* but the association may really be formed by both A and B converging towards a point between them, or, in short, mimicking each other. The acceleration of the process which in many cases would result, must of itself be an advantage. Now if the grouping of kindred inedible forms in associations of this kind is beneficial, it would seem that the benefit might extend to members of families far removed from one another, like the three now under discussion, as well as of the same family or genus;* the only requisites being (1) that all should be more or less inedible, and (2) that all should have patterns capable of assimilation to one another. Nor does there seem to be any reason why a *mutual* convergence of the kind indicated should not take place under these conditions also. With respect to (1), it has, I think, nearly always been assumed that the *Pierinæ* which resemble the members of other families are edible; and this is no doubt the case with the numerous members of the genus *Dismorphia* † (*Leptalis* of Dalman), which were among the first to attract notice to the subject of Mimicry in general. But no direct proof seems to exist that the species of *Euterpe* and *Pereute* now under discussion are edible; and indeed Mr. Wallace considers (Trans. Ent. Soc. Lond., 3rd series, iv., pp. 309, 310; Darwinism, 2nd ed., 1889,

* Such an association is already well known to occur between *Heliconidæ* and *Danaidæ*.

† This, however, has been questioned by Mr. Beddard, who cites some observations of Scudder as tending to show the contrary. See "Animal Coloration," 1892, p. 215.

p. 244) that the genus *Delias* (*Thyca* of Wallengren), which is probably nearly related to *Euterpe* and *Pereute*, possesses a disagreeable flavour, or some other special means of protection. If this is shared by its American relatives, the first of the above requirements would be satisfied, while the second (2) has been shown to be met, in the special instance of the red basal patches, by the occasional presence of somewhat similar spots or patches (whose origin is not now under discussion) in other species of both the Papilionine and Heliconine groups, which afford quite sufficient material for the assimilative process to work upon. Until, therefore, direct proof is forthcoming of the edible qualities of the Pierines in question, it will not be unreasonable to suppose that they have joined an "inedible association," and to attribute this curious agreement in a detail of pattern between members of such diverse groups to the operation of what may perhaps be called "reciprocal mimicry."* The Pierines have no doubt moved furthest from their original form, having in most respects clothed themselves in Papilionine and Heliconine colours, but the latter have themselves advanced some way to meet the Pierines, in adopting from them a more distinct and characteristic employment of the red basal patches.†

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* This, it will be seen, is distinct from "convergence" in the usual sense, inasmuch as that term has hitherto been employed (as by Poulton, "Colours of Animals," 1890, p. 195) to signify the assimilation of one form to another, rather than the mutual approach by two forms to a mean between them.

† Fritz Müller notes ("Kosmos," 1879, p. 100, and translation by Meldola, Proc. Ent. Soc. Lond., 1879, p. xxiv.) that "in the province of Santa Catharina, *Euterpe tereas* is common in the forest-paths almost throughout the entire year, while its model, *Papilio nephalion*, is, on the other hand, a rare butterfly." This is so far in favour of the supposition that the resemblance is not due to mimicry by the Pierine, at least in the strict sense.

There is one more piece of evidence that seems to favour the conclusion arrived at above. So far as I am aware no explanation has yet been offered of the fact that it is the females and not the males of *Papilio polymetus*, *P. zacynthus*, etc., that are resembled by *Euterpe tereas* and *E. critias*; whereas the males, which display brighter colours, afford at least as good if not better models for imitation. I would suggest that this is really due to "reciprocal mimicry." The protection gained by the resemblance between the Pierines and Papilios is not all on the side of the Pierines, but mutual; and the female Papilios have, as is usual, felt the need of it more urgently than the males. For this reason the female

Euterpe theano and *E. eurytele* present us with another kind of departure from the ordinary Pierine condition, the latter being an excellent copy of *Lycorea atergatis* and *Ceratinia* (*Ithomia*) *dionæa;* while *E. theano* exhibits the form of *E. eurytele* with a coloration much like that of *Pereute charops* ♂.

We find then that, thus far back in the growth of the Pierine stock, a large section has been diverted under the influence of mimicry from the regular course of development of the Pierine pattern; and in order to continue the history of the latter, we must retrace our steps and take up the thread where we left it before beginning to discuss the mimetic forms of *Pereute* and *Euterpe*.

Although it does not appear that the Old World can show any truly Pierine form so ancient as *Eucheira socialis,* there does exist a genus which seems to represent in the East nearly the same stage of development as *Catasticta, Leodonta, Pereute,* and *Euterpe* in the West. This is the genus *Delias,* the close relationship of which with the western forms mentioned has been indicated by Doubleday and Westwood (Genera of Diurnal Lepidoptera, vol. i., p. 33), and more distinctly suggested by Wallace (Trans. Ent. Soc. Lond., 3rd series, iv., p. 344).* The pattern of *Delias belladonna* is essentially similar to that of the early *Catastictas,* consisting as it does of a dark ground-colour relieved by paler touches in the interspaces, between which touches the ground-colour is already beginning to show a rudimentary division into a marginal and submarginal chain with a vaguely indicated discoidal patch in each wing. On the underside we have the same pattern in a slightly more distinct form; while, as in *Catasticta,* the pale areas of the hindwing and the apical region of the forewing are furnished with yellow streaks. The red basal patches, so characteristic of

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Papilios have been led to meet the Pierines by discarding, or at any rate by not adopting, the bright metallic blues and greens that ornament the other sex. This was no doubt a shorter and easier way to the formation of an "inedible association," than would have been the acquisition by the Pierines of colours more nearly resembling those of the male Papilios.

* *Delias* agrees closely in neuration with *Pereute* and *Leodonta.* See Butler, Cist. Entom., i., p. 40. Staudinger and Schatz, "Exot. Schmetterl.," 1892, Theil. ii., p. 63.

Catasticta and its allies, are not represented in *D. belladonna,* but in all the members of the *pasithoe* group they are not only present, but have become a very conspicuous feature in the coloration. It is not difficult to bring the other markings of *D. pasithoe, D. thisbe* and their allies into relation with those of *D. belladonna,* though the dark series S and M are as a rule less clearly indicated. The *pasithoe* and *belladonna* groups of *Delias* may thus be considered as on the whole the most ancient.* In the well-known *D. eucharis* we have the series S and M complete; the female, as is usual, showing less departure than the male from the more generalised form. As in *Catasticta,* no sooner have the dark series emerged into distinct existence than they begin to disappear; they are much less recognizable in *D. hyparete* and *D. agostina* than in *D. eucharis,* and in *D. hierte* they reach the vanishing point. *D. eucharis* and its immediate allies follow the early condition of *Delias* in having the interspaces on the underside of the hindwing more or less filled in with yellow, but they depart from it in having lost the red basal patches, and in possessing a conspicuous submarginal band of red spots (series I) between the dark series S and M; these are best seen in *D. eucharis* itself. An early stage of this red series is probably present in *D. cœneus* and the closely allied *D. philotis,* which seem to be linked with the still more primitive butterflies of the *pasithoe* group through such forms as *D. belisama* and *D. descombesi* (see p. 284). Regarding then *D. cœneus* as a new starting-point, we may trace from it in one direction the Indian group headed by *D. eucharis,* and in another the Australian forms *D. aganippe, D. harpalyce,* and *D. nigrina.* It is to be observed that both *D. eucharis* and *D. aganippe,* though probably more recent than *D. cœneus* so far as regards the underside of the hindwing, nevertheless retain in other respects more of the primitive pattern; from which we may probably conclude that some form now lost, rather than *D. cœneus* itself, supplies the true link with the *belisama* and *pasithoe* groups, while *D. cœneus* and *D. philotis* survive to show how "series I" acquired in

* I follow, in nearly every particular, Mr. Wallace's division of this genus into groups. See Trans. Ent. Soc. Lond., 3rd series, iv., p. 344, etc.

the *eucharis* and *aganippe* forms its conspicuous character. I have little doubt that the curious form *D. aganippe* is one of the oldest existing species of *Delias* in the Australian region, inferring this from its retention of the primitive series S and M with the discoidal patch in the forewing in fairly distinct form, from the presence of yellow streaks in the interspaces of the under surface, and from the occurrence of a basal red spot in the pre-costal space of the underside of the hindwing. Many of these points assimilate it to the *pasithoe* group, and even more closely to *D. belladonna.** *D. harpalyce* and *D. nigrina* seem to follow naturally on from *D. aganippe,* though in respect of the *costal* red they are perhaps a little nearer the still more primitive *D. belisama.* Another Australian offshoot of the *D. cœneus* stock is probably represented by *D. argenthona, D. mysis, D. isse,* and *D. dorimene.* The Indo-Malayan and Australian *nysa* group is probably derived from the *pasithoe* and *belladonna* groups through *D. orphne* and *D. momea.* It would be most interesting to attempt to trace in detail the phylogenetic history of the whole of this extensive genus, but it must here suffice to have indicated what appear to be the principal lines of derivation. Two points of analogy with the kindred neotropical genera may be noted before we pass on. The first is that although the invasion of a paler tint does in *Delias* tend to split the original ground-colour into marginal and submarginal series quite similar to those of *Catasticta,* and though these series in various stages of development and suppression, as also in *Catasticta,* meet us here and there throughout the entire genus, yet in many cases the series never emerge in any recognizable form, and there seems in several species a tendency for the white invasion to begin near the bases of the wings, and simply sweep the dark ground-colour away towards the margins. Even in these cases, however (as in *D. belisama* and *D. descombesi*), the females, on the underside, will usually show some indication of the primitive series. The second point to be noted is the way in which the resources of Pierine coloration are taxed to give the insects of this genus a brilliant appearance. As in the case of some of their neotropical congeners, this is effected not so much

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* See Wallace in Trans. Ent. Soc. Lond., 3rd series, iv., p. 349.

by the importation of any new feature as by the brightening up and extension of features already present, and indeed often common to the whole subfamily. The reason for this ornamentation is doubtless the same in both cases—namely, to call attention to inedible qualities. The Eastern genus, however, seems to have itself become a model for mimicry (Wallace in Trans. Ent. Soc. Lond., 3rd series, iv., pp. 309, 344), while the Western genera have modified their ancestral form in order to join an alien company of inedible insects.

The genus *Prioneris,* though differing slightly from *Delias* in neuration and other structural characters, is probably nearly akin to it, and represents, so far as the colouring is concerned, a similar degree of antiquity in the Pierine stock. The close resemblance of pattern between different species of *Delias* and *Prioneris,* to which reference has already been made (pp. 258, 284, etc.), is no doubt a true case of mimicry, but represents probably the result rather of arrested divergence than of the acquisition by *Prioneris* of new imitative features.

The two groups that have just been discussed, namely, those formed by *Delias* and *Prioneris* in the Old World, and by *Catasticta, Leodonta, Euterpe,* and *Pereute* in the New, thus constitute together a second grade, as it were, in Pierine development. The only earlier species yet mentioned is *Eucheira socialis,* but there exist certain other forms which appear to be but little inferior to that insect in antiquity; and to these, with *Eucheira,* the name of "Pierines of the first grade" may be applied. One of the forms now referred to is *Metaporia agathon.* This remarkable insect is probably the representative of an ancient group of Pierines, among which were to be found the common ancestors of the two second-grade assemblages already mentioned, and which, no doubt, supplied the link at present wanting between *Eucheira* and *Catasticta.* The relation of *Metaporia* with the Eastern assemblage is more direct than with the Western, for although it offers points of structural difference from *Delias,* it shows, nevertheless, a condition of the primitive Pierine pattern which is in all essentials identical with that of the earlier kinds of that genus. The correspondence of its markings on the upper surface with those of *Delias belladonna* and *D. eucharis* is at once evident, and, like *D. belladonna,* it has a patch of bright

yellow in the precostal space on the under surface of the lower wings. This, however, is usually confined to the inner division of the space.* Mr. Wallace† considers that *Metaporia agathon* forms with *Pontia nabellica* the fragments of an extensive natural group. He also points out the readiness with which the pattern of *M. agathon* can be traced through *P. nabellica*, *P. soracta*, and *P. hippia*, to its final disappearance in *P. cratægi*. In this range of species, to which may be added *P. oberthüri*, *P. leucodice*, *P. belucha*, and others, we recognise the now familiar phenomena of the emergence, establishment, and evanescence of a marginal and submarginal series of spots, together with a discoidal patch, formed out of relics of an original dark ground-colour. Another primitive Pierine feature, namely the persistence of dark ground-colour along the course of the nervures and nervules, is found throughout the group; and in *P. cratægi* survives the disappearance of almost every other indication of the original coloration.

The line thus marked out ends with *P. cratægi*; but in another direction there is little difficulty in linking *Pontia* with *Eucheira*, and so demonstrating the intimate connection with one another of the three last-named genera. Thus *Pontia* recalls *Eucheira* by the outline of its wings, especially the concave costal margin,‡ and in pattern *P. nabellica* shows no very great departure from the same genus. But a more striking sign of affinity exists in the common larval habitation, which, though merely rudimentary in *P. cratægi*, and belonging only to the early larval stages, is no doubt a degenerate or undeveloped form of the elaborate silken nest constructed by *E. socialis*. Webs of a structure apparently comparable with the latter are made by *Neophasia terlootii* and an allied species mentioned (though not described) by Behr.§ The affinity of the two latter insects with the genus *Pontia* appears certain; and though Behr is perhaps wrong in making them con-

* One specimen of *M. agathon* in Coll. Brit. Mus. has a few orange scales in the *outer* division of the precostal space as well.

† Trans. Ent. Soc. Lond., 3rd series, iv., p. 313.

‡ Noticed by Staudinger and Schatz, who compare it to that of *Parnassius*, Exot. Schmetterl., Th. ii., p. 62.

§ Trans. Amer. Ent. Soc., 1869, p. 303; Proc. Calif. Acad. Sci., second series, vol. ii., 1890, p. 91.

generic with *E. socialis* (which he does not seem to have seen.),* his description, nevertheless, renders it extremely probable that they are more closely related to that species than any other known butterfly. The Pierines of the first grade may accordingly be said to consist of *Eucheira*, with Behr's two "*Neophasias*," *Pontia* and *Metaporia*. The prevalent larval habit of spinning is no doubt an indication of the high antiquity of the group, and suggests, as do other features, a relationship with the Parnassids. This suggestion is further borne out by the aspect of *Mesapia peloria*, which is no doubt an offshoot of the genus *Pontia*. But such relationship is certainly of no close or direct kind, and is probably only referable to an extremely remote ancestor of the two subfamilies.†

Leaving the genus *Pontia* for a time, we may make a fresh start with *Metaporia agathon*, from which point it is not difficult to trace another principal stem, with numerous and important ramifications. The females of several species of Mr. Moore's genus *Huphina*, for instance *H. phryne* ♀, show what is to all intents and purposes the same pattern as *M. agathon* (Figs. 7, 8); and the males differ only or chiefly by the more ready admission of the white invasion, at the expense of the remains of dark ground-colour. The pattern of such a form as *H. nama* ♀, seems at first sight to belong to a different category, but a very good transition from that of *M. agathon* is afforded by *H. eperia* ♀, which shows how the arrangement of white patches in *H. nama* ♀ has grown out of the discal and cellular white, while the more marginal series I sinks gradually into the background, and with its disappearance the two dark series S and M lose of course their distinctive character. In one ancestral point, namely the filling up to a greater or less extent of the interspaces of the hindwing underside with yellow, *Huphina* shows a closer resemblance to *Delias* and *Prioneris* than to *M. agathon*, in which insect this feature is only slightly indicated. In many species

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* *N. menapia*, included by Behr in the same genus, differs from *Eucheira* is neuration and other points.

† *Davidina armandi* has been spoken of as a transitional form. But, as remarked by Staudinger and Schatz (*op. cit.*, Th. ii., p. 57), it is shown by Oberthür's figure (Etudes, iv., pl. ii, fig. 1) to be without any of the points characteristic of the Papilionidæ.

of *Huphina* the yellow is very vivid, in some it is warmed into a rich orange, and it not infrequently, as in *H. naomi*, *H. lea*, and *H. judith*, appears on the upper surface as well.

From the pattern of *Huphina* to that of *Catophaga* the passage is easy through such species as *H. cassida*, *H. nabis*, *C. paulina* (Fig. 9), and *C. ega*. In the latter genus, as in the former, the dark ground-colour is retained in much larger measure by the females than by the males; the latter indeed (as in most specimens of *C. galena* ♂) have often lost it altogether. Other marks of specialization shown by the male *Catophagas* are the sharply-pointed shape of the wings, and, above all, the presence of a tuft of long hairs springing from the base of each of the anal valves. All these characters belong equally to the next genus *Appias* (which indeed is not easily to be distinguished from *Catophaga*), though here the specialization of the males has in many forms been carried to a much greater extent, and is occasionally in some respects shared by the females, as in *A. nero*. In this insect the female shows the remains of the usual dark marginal and submarginal series standing out upon a ground colour of rich red almost as brilliant as that of the male, and altogether different from the ordinary Pierine white or yellow. The females, however, of *A. celestina*, *A. clementina* (Fig. 10), and others, do not depart, like the males, from the ordinary facies of the group, * and are indeed, barely distinguishable from the females of *C. jacquinotii*, *C. alope*, and other species of *Catophaga*. The assemblage of species united by Mr. Distant as *Saletara* (including *S. panda*, *S. cycinna*, etc.) is undoubtedly an offshoot from the *celestina* group of *Appias*.

In the three last-mentioned genera, although the two series S and M are generally more or less traceable, and although in most cases a decided remnant of ancestral black persists along the costa of the forewing, there is as a rule no relic of the original ground-colour in the region of the disco-cellular nervules; that is to say, there is no discoidal spot or patch. In *Hiposcritia*, however, which is apparently an early and purely Indian offshoot of *Catophaga*, some species (as *H. pandione*) exhibit an incipient discoidal patch, still in connection with

* See Wallace, Trans. Ent. Soc. Lond., 3rd series, iv., p. 301.

the dark-coloured costa; in others (as *H. lalage*) this has become a distinct discoidal spot (Fig. 11). *Hiposcritia,* by its anal tufts, belongs decidedly to the *Catophaga* and *Appias* group; but the shape of its wings and the occasional persistence of dark ground-colour about the discocellular nervules indicate that its origin is to be placed somewhat far back towards *Huphina* and *Metaporia.*

Starting again from *Metaporia* and *Pontia,* we find in the small Siberian *P. leucodice* an unmistakable link between these genera and *Synchloe.* In *S. callidice,* which perhaps come nearest to *Pontia,* the female shows S and M in a well-defined condition, together with a large distinct discoidal patch; the nervures and nervules are also in many instances clothed with black scales. From *S. callidice* we can advance in one direction through *S. chloridice* to *S. glauconome, S. johnstonii,* and *S. hellica;* while *S. daplidice* and its immediate allies form another slightly divergent branch from *S. chloridice. S. callidice* again in all probability marks the point at or near which the assemblage of species grouped as *Ganoris* leave the main *Synchloe* stem; *G. napi* being no doubt the species which is closest to the original stock, as is shown by the large persistence of S and M, the tendency towards blackening of the nervures, the occasional indication of a discoidal spot, and the peculiar coloration of the underside of the hindwings. It is noticeable that *Ganoris* generally, including *G. napi,* retains the precostal yellow streak, which, though present in most species of *Synchloe,* happens to be absent in *S. callidice.*

Most species of the genus *Tatochila* strongly resemble *Pontia* in pattern (the resemblance between *Tatochila* and *P. leucodice* has been pointed out by Mr. Butler, Proc. Zool. Soc., 1872, p. 62), while *T. autodice* ♀ comes nearer to *M. agathon* than does any species of *Synchloe.* The whole neuration of *Tatochila* is very similar to that of *Pontia;* and even the peculiar arching of the 1st subcostal of the hindwing (well seen in *P. cratægi*) is a noticeable feature in *T. theodice* and other members of the same genus.* *Tatochila* may, therefore, be considered to be a derivative from the *Pontia* stem at a point somewhat further back than the existing species of *Synchloe.*

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* See Mr. Butler's figures in Cist. Entom., vol. i., pl. iii., figs. 7 and 9.

A comparison of *Tatochila* (especially of *T. theodice*) with *Phulia nymphula* will show an almost exact identity of pattern, the correspondence extending even to the chevron-shaped spots of S in the hindwing, and to the peculiar triple striation of the nervules on the under surface. The neuration of *Phulia* is distinct, but not really far removed from that of *Tatochila,* some species of which show a near approach to its most remarkable feature; viz., the emission of the second radial from the subcostal, and the consequent obliteration of the upper disco-cellular. *Phulia* again is closely allied in structure with Mr. Moore's genus *Baltia,** which, however, retains the short 3rd subcostal nervule lost by *Phulia* and several species of *Synchloe. Phulia* and *Baltia* are thus, in all probability, the terminal twigs of another branch which issued from the *Pontia* stem between the departure of *Tatochila* and *Synchloe. Neophasia menapia* appears to me to be an offshoot of the same stem at an earlier stage than *Tatochila.* It may possibly belong to the *Eucheira* group, but it is not known to make a social web,† and Behr gives no real grounds for making it congeneric with "*N.*" *terlootii.* As above noted, its neuration is very distinct from that of *Eucheira.*

The African species of the genus *Mylothris*‡ appear to hold a somewhat isolated position. Their neuration shows points of likeness with the equally isolated Australian genus *Elodina* and the widely-spread and probably ancient *Nychitona,*‖ which genera they also somewhat resemble in texture of wing. In pattern they are chiefly remarkable for the strong and distinct development of series M, and of the precostal orange-red

* Moore's type is "*Mesapia*" *shawii* of Bates, which is certainly generically distinct from *M. peloria*, and much nearer *Synchloe.* The butterfly described by Moore in Proc. Zool. Soc., 1882, p. 234, as *Synchloe butleri* is undoubtedly a *Baltia.*

† Stretch, however (Papilio, ii, pp. 106, 107), describes the larvæ of *N. menapia* as suspending themselves from great heights at the end of long silken threads. Even the pupæ were, in some cases, suspended. It is probable that the numerous threads covering the bark of the trees seen by Stretch (*ibid.*), were also made by these larvæ.

‡ I cannot but agree with Mr. Trimen (South African Butterflies, 1887, vol. iii., p. 29) that the American *P. pyrrha*, Fabr., and allies, are not generically akin to the African *M. agathina*, *M. chloris*, etc., with which Mr. Butler unites them on account of their correspondence in neuration (Proc. Zool. Soc., 1892, pp. 37, 38).

‖ Distant, Rhopalocera Malayana, 1882—1886, p. 287.

on the underside of the hindwing. We may, perhaps, regard all three genera as relics of an ancient fauna of the Eastern Hemisphere coeval with the earliest forms represented by the present *Delias* stock, and anterior to the various branches which have diverged from that genus or from *Metaporia*. The precostal orange suggests a kinship with *Delias* on the part of *Mylothris*, though no such link exists in the case of the other two genera, and, as pointed out by Mr. Trimen, who considers *Mylothris* and *Thyca* (*Delias*) to be allied genera, the former genus, like the latter, undoubtedly contains subjects of mimicry by *Pierinæ* of other groups. Thus, "The imitation of *M. agathina* by *P. thysa*, Hopff., is deceptively close in both sexes, and *M. poppæa*, Cram., is similarly copied by *P. rhodope*, Fabr., on the West Coast. *M. agathina* is also mimicked by the female *Eronia argia*, Fabr."*

We now have to deal with the genus *Belenois*, which presents some special difficulties. In the first place, we find an assemblage of species (*B. lasti*, *B. nagare*, *B. majungana*, and *B. isokari*) from East Africa and Madagascar, with respect to which Messrs. Grose Smith and Kirby, after noting that they are now placed with *Phrissura* in the Collection of the British Museum, go on to observe that they "differ entirely in neuration from the types of *Phrissura*, agreeing in this particular with *Belenois*, in which genus we prefer to include them."† The type of Mr. Butler's *Phrissura* is apparently *P. illana*, Feld.,‡ and in 1872 (Proc. Zool. Soc., 1872, p. 51) the only other species of *Phrissura* admitted by Mr. Butler was *P. polisma*, which is undoubtedly a very near relative of *P. illana*. Both of these species offer differences in neuration from *B. lasti* and its allies.|| Now,

* South African Butterflies, vol. iii., p. 39 (1887).

† Rhopalocera Exotica, Oct. 1892.

‡ Mr. Butler first gave it as *P. cynis* (Cist. Entom., iii., 1870, p. 49), but afterwards corrected it to *P. illana* (Trans. Ent. Soc. Lond., 1871, p. 171). Mr. Distant has since made *cynis* the type of his new genus *Udaiana*. (Rhopal. Malayan., 1882—1886, p. 286 and note).

|| In *P. illana* (forewing) the discoidal cell is unusually short, the second subcostal starts from the end of the cell, and the second and third median nervules come off near together; in *B. lasti* the cell is of the ordinary length, the second subcostal is emitted before the end of the cell, and the second and third median nervules do not start particularly near together.

however, certain forms are included under *Phrissura* in the Collection of the British Museum (*P. phaola, P. sylvia, P. eudoxia*, etc.) which appear to me to agree in structural characters with *B. lasti*, and to differ from *P. illana*. If, therefore, Messrs. Grose Smith and Kirby are right (which I do not doubt) in separating *B. lasti*, etc., from *Phrissura* as represented by *P. illana*, I am strongly of opinion that *P. phaola, P. sylvia, P. eudoxia*,* and *P. coniata* should go with them; and to this assemblage I would add every so-called *Belenois* that is furnished with anal tufts, together with "*Belenois*" or "*Glutophrissa*" *saba*. We should then have a natural group of African and Malagasy Pierines, between which there would exist no assignable difference in structure, while they would be all alike characterised by the possession of anal tufts like those of *Catophaga* and *Appias*. They may, perhaps, be considered as a section of *Belenois*, but to my mind they seem by their neuration, no less than by the obvious character of the anal tufts, to come much nearer to *Appias*, of which genus I am disposed to regard them as an African offshoot. The South American species *Glutophrissa poeyi, G. margarita, G. castalia*, etc., are very closely related to the present section.†

Although the structural affinity of the forms that have just been discussed with each other and with *Appias* seems undeniable, there is no doubt that in pattern they mostly show a marked divergence from that genus. This appears to be due to mimicry, the models for which are usually supplied by the genus *Mylothris*. Thus *B. lasti* is said by Messrs. Grose Smith and Kirby to be "nearest to *B. trimenia*, Butl."; the latter, however, is a true *Mylothris* with the characteristic neuration of that genus. Considerable resemblance also obtains (as mentioned above, p. 308) between *P. rhodope*, Fabr., and *M.*

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* *P. eudoxia*, Cram., is apparently identical with *P. sylvia* ♀, Fabr.

† Mr. Wallace (*loc. cit.*, p. 312) includes these American and African forms with *Appias, Catophaga*, and *Hiposcritia* in his genus *Tachyris*. For the purposes of the present paper it will perhaps be sufficient if I refer to the American and African species with Appias-like structure and anal tufts collectively as "*Phrissura B*," while designating *polisma* and *illana* as "*Phrissura A*."

poppea, Cram.* The peculiar facies of *G. saba* ♀ seems to be most likely due to mimicry of *Nyctemera apicalis*, a protected moth. Those members of the group that have not been affected by mimicry retain few traces of the original ground-colour, and present very much the appearance of an ordinary male *Appias* (*G. saba* ♂, *G. castalia*, etc.).

The other species usually included under *Belenois*, besides differing in points of structure† from those just discussed, show as a rule a greater persistence of dark ground-colour. Both S and M are usually present in fair development, either separate or fused, and the discoidal patch on the forewings is generally well marked. The markings in several species show a strong resemblance to those of *Synchloe hellica* and *S. johnstonii*; but notwithstanding this, I am disposed to think that *Belenois* proper really represents an offshoot of another part of the Old World Pierine stem, that, namely, represented by *Delias* and *Prioneris*. The distribution of dark and light ground-colour in such species as *B mesentina* might easily be derived from those of *D. belladonna* and *D. eucharis*, and the underside of the hindwing in this and other forms of *Belenois* offers only slight modifications from that of *D. belladonna*. *B. peristhene* exhibits a curious resemblance on both surfaces to *D. nysa* which may perhaps be due to mimicry, although the ranges of the two insects only coincide for a small part of their extent; it is not improbably in any case an indication of real affinity. In neuration, those species of

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* I adopt Mr. Trimen's unravelling of the strange confusion that surrounds the synonymy of *rhodope*, Fabr., and *poppea*, Cram. (South African Butterflies, vol. iii., p. 35, and note). The upshot no doubt is that a true *Mylothris* (*Papilio poppea* of Cramer according to Mr. Trimen) is closely copied by at least one Pierine of the "*B*" group of *Phrissura* (*Papilio rhodope* of Fabricius according to the same authority). I do not propose to embark upon the question further than to observe that the "Synonymic Catalogue" identifies the two, and that Mr. Trimen himself unfortunately speaks of *rhodope* in the text, when he must mean *poppea* (ibid. p. 35).

† Negatively by the absence of anal tufts, positively by the presence (in many) of anal hooks, also by the straight direction and greater relative length of the upper disco-cellular nervule in the forewing. In many species of this group, which we may designate *Belenois* proper, the first subcostal branch anastomoses with the costal.

Belenois in which the first subcostal is distinct are very near *Prioneris*, and the remainder seem to approximate to *Delias* by the partial loss of a subcostal branch, as well as by the contour and direction of the disco-cellular nervules. It is to be observed that some species of *Belenois* proper, like those of the "*Phrissura B*" group, are mimics of various species of *Mylothris*, as *B. thysa* of *M. agathina*. *Pinacopteryx* is probably a collateral or derived branch of *Belenois*; the female of *P. capricornus* retains S and M on both surfaces in a well-marked condition.

We now come to a large and important group of genera which appears to take origin from the older Pierine stock at a point nearest to the genus *Synchloe*. An early stage of divergence is reached by *Teracolus*;* many species of which show the primitive series S and M, together with the discoidal spot and the precostal yellow of the underside of the hindwing. The curious genus *Herpænia* is probably a survival of the links that once united *Teracolus* with *Synchloe*; in neuration it is intermediate between the two, and in pattern, together with aberrations peculiar to itself, it shows points of contact with both. The pattern of the upper surface in *Teracolus* is easily derivable from that of *Synchloe*, the nearest approach to *Synchloe* in this respect being made by the *Idmais* group; compare, for instance, *T. dynamene* with *S. hellica* ♀. But the passage from the underside of the hindwing in *Synchloe* to that of *Teracolus* is more difficult; *Herpænia*, however, enables us to bridge over the interval very fairly, for if *H. tritogenia* and *H. lacteipennis* be interposed between *S. glauconome* and *T. puellaris* ♀, the abruptness of the transition is removed. The pupa of *Teracolus* tends to be boat-shaped, with a sharply-pointed rostrum and large prominent wings†—which characteristics we shall find

* I follow Mr. Butler (Cist. Entom. vol. i., p. 36), with whom Mr. Trimen is in agreement (South African Butterflies, vol. iii., p. 82), in uniting *Teracolus*, *Idmais*, and *Callosune* under the single head of *Teracolus*.

† These features are not equally well developed in all species of *Teracolus*. They are very distinctly shown in pupæ of *T. evarne* (Coll. Hope); pupæ of *T. calais* (Coll. B. Mus.), on the other hand, are slender, less recurved, and nearer the *Ganoris* or *Synchloe* form. The pupa of *T. pleione* (Coll. B. Mus.) is stout, and not unlike that of *Gonepteryx rhamni*; compare Mr. Trimen's description, *op.*

in a greater or less state of development in all the genera of the particular group of Pierines now under discussion. Other features, which appear first in *Teracolus* and will be met with again later on in the history of the group, are the pinkish fringe of the wings in some species (as *T. wallengrenii,* and often in *T. protractus*) and the faint pinkish *Colias*-like spot or patch at the root of the cell in the hindwing underside of others (as *T. tripunctatus, T. cœlestis* ♀, *T. eupompe,* and *T. theogone*).

The genus *Ixias* follows easily upon *Teracolus,* the females of the two genera showing, as usual, a greater affinity in colouring than the males (compare, for instance, the males and females of *T. ione* and *I. marianne* *). Series S is often well preserved in *Ixias,* especially on the underside and in the female; the discoidal spots are also prominent, and begin on the lower surface to assume an ocellate character. In neuration, *Ixias* differs only slightly from *Teracolus*; while the pupa, as shown in drawings by Captain Boys of *I. marianne* and *I. evippe* (Coll. Hope), has the same characters as *Teracolus* in a more strongly-marked condition.

From the usual system of colours and markings in *Ixias,* there can be little doubt that that genus represents the transition from *Teracolus* to *Colias.* The underside of several species of the latter genus (for instance, *C. subaurata*) is strongly recalled by that of *I. marianne,* in which the *Colias*-like condition of the discoidal spots is one of the most noticeable features. The affinity suggested by the colour-pattern is borne out by the structure of the antennæ, which in *Ixias* show a distinct approximation to the gradually thickened form so characteristic of *Colias* and its immediate allies. The pupa in *Colias,* as in *Teracolus,* seems to vary somewhat in form; but in all known cases it shows a tendency, sometimes strongly pronounced, towards the acuminate and boat-shaped outline characteristic of this group of genera.

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cit., vol. iii., p. 82. I refrain from using the terms "wing-covers" or "wing-cases," the inapplicability of which has been shown by Prof. Poulton (Trans. Linn. Soc., 1890, series ii., vol. v., part 5, p. 188).

* Mr. Butler points out the intermediate character of the two African species, *Ixias eulimene* and *I. venatus.* Proc. Zool. Soc., 1871, p. 254.

The genus *Xanthidia* is transitional between *Colias* and *Terias,* in neuration coming nearer the latter. The pattern on the upper side is scarcely modified from that of *Colias;* on the under surface, however, S has lost much of the distinctness it possesses in so many species of the latter genus, and its relics take part in a general mottling which is very probably protective in object.

In *Terias* the resolution of series S and M, which is still visible in most of the females and many of the males of *Colias,* has usually disappeared from the upper surface; the underside of the hindwings, however, generally shows S in a somewhat modified condition. The pink edging to the wings, so characteristic of *Colias,* and occasionally visible in *Xanthidia nicippe,* is indicated in several species of *Terias,* as *T. messalina, T. delia,* and *T. rhodia.* The pupa of *Terias* is more sharply acuminate and recurved than that of *Colias* (see pupa of *T. mandarina* and *T. excavata* in Coll. B. Mus.).

Sphænogona presents in pattern no marked differences from *Terias,* with which genus it is so closely allied. *S. gratiosa,* like *T. agave, X. nicippe,* and some other species of these genera, shows a relic of the pinkish *Colias*-patch at the root of the cell on the underside of the hindwing. In neuration, *Sphænogona,* while generally resembling *Terias,* is peculiar in emitting the first and second subcostal branches of the hindwing from a short footstalk beyond the end of the cell. In this respect it is intermediate between *Terias* and *Leucidea,* which latter genus presents no markings to guide us, but has no doubt taken its origin directly or indirectly from *Terias.** Another probable descendant of *Terias* is the genus *Nathalis,* which agrees very fairly with *Terias* in neuration, except that it wants one nervule in the forewing, probably a branch of the subcostal. There is a striking resemblance of pattern between *N. iola* and *T. elathea* ♂. In the absence of paronychia *Nathalis* reverts to the condition of *Colias.*

Pyrisitia seems to represent an early offshoot of the stem leading from *Colias* to *Terias.* In most points it

* Staudinger and Schatz (*op. cit.*, Theil. ii., p. 66, etc.) consider *Leucidea* to be more closely related to *Pontia* (*Nychitona*) than to *Eurema* (*Terias*). The balance of evidence seems to me to be against this view.

agrees with the latter genus, but in the position of the subcostal nervules of the hindwing it retains the condition of the former.

A fresh departure from *Colias* is headed by the genus *Meganostoma*, which offers a close resemblance to *Colias* in both structure and pattern.* The series S and M, fairly distinct in the female of *M. philippa*, are also indicated on the upper surface in the males of some of the species. In the males of some other species they are fused above, but in all they are distinguishable beneath. In the outline of the wings *Meganostoma* shows a close approach to *Gonepteryx*, from which genus indeed the females of some of the species are hardly to be distinguished.

From *Gonepteryx* the line passes on to *Amynthia* and *Rhodocera*. All these genera retain many *Colias*-like points, particularly the pinkish patch at the apex of the cell on the hindwing undersurface. The males of the two latter, like those of *Meganostoma* and many species of *Colias*, also possess the well-known patches of raised scales above the subcostal nervure of the hindwing; and in the same two genera is seen for the first time the contrast between areas of flat and raised scales over the whole upper surface of the wings which is so conspicuous a feature in *Catopsilia*, *Phœbis*, and *Callidryas*.

Dercas appears to be an Indian offshoot of *Gonepteryx*. A good transition from the latter to the former is afforded by *D. wallichii*, as pointed out by Mr. Wallace, Trans. Ent. Soc. Lond., 3rd series, iv., p. 398. *Kricogonia* is probably an analogous derived form in the Neotropical Region.

The Eastern genus *Catopsilia* forms with the Western *Callidryas*, *Aphrissa*, *Metura*, and *Phœbis*, a group which clearly belongs to the present section. Their structure and coloration relate them closely to *Gonepteryx*, though in some respects they show signs of a more ancient

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* Mr. Butler (Cist. Entom., iii., p. 46) describes the neuration in the forewing of *Meganostoma* as being like that of *Gonepteryx*, "excepting that the second subcostal is emitted just before the end of the cell." In some individuals, at any rate, the second subcostal is emitted *at* the end of the cell, and in *M. cesonia* it may even be thrown off *after* the end of the cell, as often in *Colias*. This indeed is the condition represented in Cist. Entom., vol. i., pl. ii., fig. 4.

ancestry. The retention of the pink patch on the underside of the hindwing, and (in several species) of the pink fringe, brings them near to *Colias*; to which they also approximate by the form of the antennæ, by the very general occurrence of special patches of raised scales on the hindwing of the males, by the frequent presence, especially in the females, of the series S and M and the discoidal spots in a more developed condition than that characteristic of *Gonepteryx*, and by the common tendency of the latter spots on the lower surface towards ocellation. The oldest forms of the whole group appear to be those contained in the genus *Catopsilia*. *C. florella*, for example, is very closely related to *Gonepteryx*, and still more nearly to *Amynthia*, with which it corresponds in colour and in texture of wings (compare especially the undersides of *C. florella* ♂ and *A. clorinde*). The peculiar thickening of the nervures, especially the subcostal and median, on the under surface of the hindwing, which in *Gonepteryx* and *Amynthia* give almost the effect of a folding of the surface, is plainly visible in *C. florella*. In neuration, *C. florella* agrees minutely with *A. clorinde*. Another indication of the superior antiquity of the Eastern *Catopsilia* as compared with the Western *Callidryas* is found in the shape of the pupa. This in *Catopsilia* (as remarked by Mr. Trimen, *op. cit.*, vol. iii., p. 184) is only moderately acuminate and slightly recurved, thus showing no very great departure from the *Colias* and *Gonepteryx* form; in *Callidryas*, however, so far as is known, it is always very sharply acuminate and strongly recurved, showing an exaggeration of the "boat-shaped" condition almost as marked, in a different way, as that of *Euchloe*.* The *Colias*-like pink edging appears also to be found more frequently in *Catopsilia* than in *Callidryas* (though it occurs in *Callidryas sennæ*); and while the *Colias*-like spot at the root of the cell on the underside of the hindwing occurs in both the Eastern and the Western divisions of the group, it has in the latter lost the ancestral pink tinge

* I agree with Mr. Butler that the pupa figured in Lep. Exot., pl. xlv., fig. 4*a*, as *P. agarithe* is very probably that of *C. philea*. It closely resembles a pupa of *C. eubule* in the Hope Collection, which last exactly corresponds with Burmeister's figure in the "Atlas de la Description Physique de la Rép. Argent.," 1880, pl. v, fig. 2.

which it usually retains in the former. It is not very easy to form an opinion as to the relative antiquity of the four Western genera; if we are to judge from the pupæ, so far as they are known, it would seem that *Aphrissa* has undergone less modification than either *Phœbis* or *Callidryas*. Another possible indication of the greater antiquity of *Aphrissa* is afforded by the shape and size of the palpi, which in this genus, especially in the females, show less departure than is the case in either *Phœbis*, *Metura*, or *Callidryas*, from the *Colias* and *Gonepteryx* type. *Phœbis* with its offshoot *Metura*, from which it differs only in the contour of the wings, is probably the most highly specialised genus of all; this being shown by the possession of a tuft of long hairs on the hindwing of the male, which is not found in *Aphrissa* and *Callidryas*, and by the absence in most species of nearly all indication of dark ground-colour from the upper surface. It is remarkable that the Western genera just treated of are less closely akin to the South American *Amynthia* than is the Eastern genus *Catopsilia*, and especially the African *C. florella*.

The genus *Eronia* seems to represent a branch of the present section which leaves the main stem somewhere between the points marked by *Teracolus* and *Ixias*. With the exception of the presence of a fifth subcostal in the forewing (which, however, is sometimes wanting), the neuration of *Eronia* agrees fairly with that of *Teracolus*. The antennæ in *Eronia* differ in different species, but are all intermediate between the *Teracolus* and the *Colias* type; and the pupa of *E. cleodora*, with its very convex and prominent keel, is like that of one of the stout forms of *Teracolus*, e.g., *T. evarne*. The assemblage of species distinguished by Mr. Butler as *Nepheronia* is probably older than *Eronia* proper, as is shown by the tendency of its antennæ to terminate in a definite club, like the more ancient genus *Teracolus*. *N. thalassina* also retains a primitive Pierine feature in the yellow precostal streak of the hindwing underside, which again is found in some species of *Teracolus*. *Eronia* proper, on the other hand, is slightly nearer to *Teracolus* in neuration. The curious *Eronia* (?) *lucasii* from Madagascar, which has only four subcostal nervules in the forewing, and whose antennæ are slender, with a definite club, is probably one of the oldest and most

generalised members of the *Eronia* and *Nepheronia* group now extant.*

The last-named insect presents points of resemblance with *Hebomoia,* which again seems to be an offshoot of the same stem, that, namely, leading from *Teracolus* towards *Ixias* and *Colias.* The pupa of *Hebomoia glaucippe,* as figured by Horsfield (E. I. C. Catalogue, see Distant, Rhopal. Malayana, 1882—6, p. 283) and Moore (Lep. Ceylon, 1880—1, pl. 49, fig. 1*b*), is stout, moderately acuminate, and much recurved, in which particulars it agrees well with the pupa of *Ixias.*

Most of the insects of the genera *Eronia, Nepheronia,* and *Hebomoia,* retain in greater or less measure some portions of the primitive marginal and submarginal series. These, as usual, are most often to be met with in the females, and in several species of *Nepheronia* are utilised in the formation of mimetic patterns modelled on those of various Danaids and sometimes of other Pierines. A noticeable feature in some members of this group, pertaining chiefly to the males, is the brightening of the pale ground colour of the apex of the forewing into a brilliant yellow or orange patch. This character is first seen in *Teracolus,* where the orange of the apex may further deepen into crimson or violet; it passes on to *Hebomoia,* to *Ixias* and to *Rhodocera*; in *Colias,* however, it gives place to a general yellow or orange suffusion of the pale ground colour, still strongest in the males.† It is found in *Eronia* (?) *lucasii* and *E. leda,* but not in other members of that genus; it is also absent in *Nepheronia.*

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* *E.* (?) *lucasii* was originally described (as *Callidryas lucasi*) by Grandidier (Rév. et Magas. de Zool., Aug. 1867, p. 273). He, however, took the female for the male, and his supposed female *C. lucasi* is really the female of *Catopsilia thauruma.* Mabille in the Hist. Phys. Nat. et Pol. de Madagascar, vol. xviii., 1887, p. 281, gives a correct description of both sexes under the name of *Eronia lucasii,* but makes no mention of Grandidier's mistakes. This species will not come into the genus *Eronia* as at present defined. By Brauer and others it has been called a *Ptychopteryx*; the latter genus, however, was characterised by Wallengren from a species of *Teracolus* (*T. subfasciatus,* Swains., Vid. Trimen, South African Butterflies, vol. iii., 1889, p. 92), and has no real claim to stand.

† In many species of the latter genus, indeed, the females may, as is well known, revert almost entirely to the ancestral white.

This last feature in coloration is again met with in *Eroessa* and *Euchloe,* the neuration of which genera corresponds pretty closely with that of *Eronia,* not only in the presence of five subcostal branches in the forewing, but also in other particulars. The general likeness between *Eronia leda* and *Euchloe belia,* Linn., is very striking, and strongly suggestive of a near affinity between them. The well-known form of the pupa in *Euchloe* is an exaggeration of that seen in *Eronia cleodora.** In some other points, however, *Euchloe* is nearer to *Colias,* as in the strong development of the discoidal spot in the primaries, and in the possession by some species of pink legs and a pink edging to the wings. This last feature is characteristic of the *charlonia* group of *Euchloe,* and is best seen in *E. lucilla.* The underside of the hindwing in the same group has very much the character of the corresponding region in *Colias palæno,* including the pale undeveloped discoidal spot. The antennæ, however, of *Euchloe* are very distinct in form from those of *Colias,* and indeed are not much nearer those of *Eronia.* On the whole it seems most likely that *Euchloe* is a somewhat aberrant branch which takes its rise from the Pierine stem at a point near the divergence from the same stem of *Hebomoia* on the one hand, and *E.* (?) *lucasii* with the rest of the *Eronia* and *Nepheronia* group on the other. The isolated form *Eroessa chilensis,* which in neuration approaches the older *Eronias* (as *E.* (?) *lucasii*) and *Hebomoia,* is perhaps a survival of a once more widely-spread and numerous assemblage, among which were to be found the immediate ancestors of the present-day *Euchloes. Zegris* seems to be a somewhat highly modified offshoot of the *Euchloe* branch.

We must now retrace our steps as far as to the group which I have called "Pierines of the second grade," those, namely, that are typified by *Delias* in the Eastern and *Catasticta* in the Western hemisphere. The latter genus with its near ally *Leodonta* forms a starting-point for a New-World division of the Pierine stem, which, if not equal in magnitude to the great division headed in the

* The pupa in *Euchloe* is not always recurved. See Edwards's figures of *Anthocharis* (*Euchloe*) *genutia* and *A. ausonides* in "Butterflies of North America." See also Schatz, Exotische Schmett., Theil ii., 1892, p. 71.

Old World by *Delias, Prioneris,* and *Metaporia,* is nevertheless of high importance and very great interest.

The first departure from the condition of *Catasticta* seems to be that taken by the butterflies of the genus *Pieris* as restricted by Butler, closely associated with which must come the American species of *Mylothris.* The underside of *Pieris locusta* exhibits a pattern which is but little removed from that of *Catasticta,* the yellow streaks and red basal patches being still apparent on the underside of the hindwing; while the upper surface of both wings is shared between the original dark and intrusive light ground colour in much the same manner as in *C. ctemene, C. corcyra,* and other species of *Catasticta.* In *Pieris* as a whole, the dark ground-colour has to a great extent disappeared from the upper surface; several species however (as *P. pylotis* and *P. buniæ*) retain a discoidal spot in the forewing, which in some, as *P. thaloe* ♀, is connected with a dark streak along the costa, and in others, as *P. demophile* ♀, is included in a larger remnant of ground-colour which passes as a dark fascia obliquely across the wing from the costa to the outer border. The underside of the hindwing in this genus tends to lose the *Catasticta*-like character preserved in *P. locusta,* in consequence of a general paling which takes effect first in the basal half and spreads outwards (as in *P. demophile*), until in such species as *P. buniæ* it reduces the wing to very much the same condition as that seen in *Ganoris brassicæ* or *G. rapi.* The ground-colour in *P. buniæ* and *P. pylotis* is indeed even paler than in these species of *Ganoris,* being without the powdering of black scales which the latter possess; the hindwing however of both *P. buniæ* and *P. pylotis* retains a discoidal spot, and, as has been already noted (pp. 287, 289, note), the predominance of the paler colouring is never so great as not to leave unmistakable relics of the yellow streaks and red basal patches.

The genus *Leptophobia* appears to be a kind of continuation of *Pieris.* The arrangement of light and dark ground-colour preserves a parallel course in the two genera, and the inclusion of the discoidal spot of the forewings in a dark fascia which passes from the costa for a greater or less distance obliquely towards the outer margin is a common feature in *Leptophobia* as well as in *Pieris.* In the present genus the underside of the hind-

wings is almost uniformly pale, but distinct indications of the primitive red patches are nevertheless still to be met with (see p. 287).

There would also seem to be little doubt that the American species allied to *M. pyrrha,* which are included by Mr. Butler* under *Mylothris,* with the neuration of which they agree, are closely related to *Pieris.* The pattern of every one has been more or less altered by mimicry, but in those males whose upper surface is unaffected by this kind of modification, the arrangement of the dark and light ground-colour is seen to present the ordinary features of *Pieris* or *Leptophobia* (compare, for instance, the upper side of *M. pyrrha* ♂ with that of *P. thaloe*). In *M. lorena* is found an oblique dark bar crossing the forewing just as in *P. demophile* and *L. stamnata,* this mark being utilised, both in *M. lorena* and the female of *M. pyrrha,* for the formation of the mimetic pattern. It has already been shown† how the primitive yellow streaks and red basal patches have been turned to account in the same direction on the underside of the hindwing, which, from the additional necessity for protection experienced by the insect when at rest with its wings closed, becomes the most important field for the mimetic process. It may be here remarked that the antennæ of these American forms, while agreeing in character with those of *Leptophobia, Pieris, Catasticta, Leodonta,* and the genera allied to these last, differ conspicuously from those of *M. agathina, M. poppea,* and the other African species of *Mylothris.*

Hesperocharis diverges somewhat widely from the genera last discussed, both in neuration and in the character of its antennæ; it retains, however, in many cases indications of the primitive marginal and submarginal dark series in a more recognizable form than any (see, for instance, the chevrons on the underside of *H. erota,* which represent series S). The yellow streaks

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* Proc. Zool. Soc., 1872, pp. 36-38. It appears to me that the neuration of the American forms of *Mylothris* is simply that of *Pieris, minus* the third subcostal nervule in the forewing, which branch is already almost obsolete in the latter genus.

† See above, p. 286. The transitional series which is there made to begin with *M. lypera* and *M. lorena* might easily be carried back to *P. thaloe,* which shows the true Pierine pattern all ready, as it were, to take on the mimetic condition of the other species.

and red basal patches, present in all species of *Hesperocharis,* are in some (as *H. nereis*) marked with special distinctness. The curious manner in which these have been made use of in *H. hirlanda* for the production of a mimetic pattern, has already been fully discussed (p. 286).

I cannot but think that *U. monuste* shows by its pattern that it stands on a level with *Pieris* as a derivative from the *Catasticta* group. Its neuration hardly differs from that of *Pieris,* and it would probably be more appropriately placed (together with its immediate allies, *U. joppe, U. suasa,* etc.) in or near that genus than with *U. cynis* in Mr. Distant's genus *Udaiana,* as at present in the National Collection.

The position of the genus *Dismorphia* is not easy to determine. The pattern of those species that appear to have undergone least modification may, however, be derived without much difficulty from *Pieris* or *Leptophobia;** and the persistence in some cases of the red basal spots has already been remarked (see p. 285). The structure of the antennæ points to the same line of ancestry. On the other hand, the very remarkable neuration is quite unlike that of *Pieris*; a certain approach to it, however, is made by *Hesperocharis,* which is almost without doubt a close ally of that genus. *Moschoneura*† is very nearly akin to *Dismorphia,* from which it differs only slightly in neuration; while the Palæarctic genus *Leptosia* has characters which link it with both.‡ We may probably regard the three last-named genera as terminal twigs of a branch now lost, which left the main stem at or near the genus *Pieris,* and of which *Hesperocharis* is a still earlier offshoot. In *Dismorphia* and a few species of *Moschoneura* much of the original colouring has been retained and modified for purposes of mimicry. In *Leptosia* and the remainder§ of *Moschoneura* this colouring has given way to the usual Pierine invasion of white.

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* A somewhat different and, as it seems to me, less probable view is advanced by F. Müller, Jenaische Zeitschr., x., pp. 1–12.

† The figure in Cistula Entomologica, vol. i., pl. iv., fig. 9, omits the second discoidal of the forewing.

‡ The forewing is nearer to *Dismorphia* and the hindwing to *Moschoneura.*

§ *Pseudopieris* of Godman and Salvin.

2. *The evidence of distribution.*

It now remains to briefly indicate the bearing of the geographical distribution of the various forms that have been mentioned upon the question of their kinship and relative antiquity.

As we have already seen, the oldest form of Pierine now extant is probably *Eucheira socialis*. This insect appears to be as limited in its geographical range as it is isolated in its zoological position, for it is found only in the mountain-ranges of Mexico, which may be considered as a southern extension of the "Rocky Mountain" division of the Nearctic Region.* Its nearest allies appear to be Behr's two species of *Neophasia* (see p. 303), which inhabit the same region with itself, and the *Pontias* and *Metaporias* of the high lands of Central Asia, most of which forms are known to retain the ancient larval habit of spinning. These facts seem to point to the conclusion that *Eucheira* is the relic of an archaic group of Pierines which once occupied the great mountain regions of both the Palæarctic and Nearctic continents, and whose immediate descendants, still represented in the East by *Metaporia* and *Pontia*, have in the West become extinct (unless Behr's *Neophasia* be a survival) after giving origin to the group of genera headed by *Catasticta*.

From one or other of these two primary stems, the Eastern or the Western, nearly the whole of the existing genera of Pierines may be derived. There are, however, a few exceptions, which, perhaps, constitute relics of an ancient Pierine fauna coeval with the groups above mentioned, but not, like them, the progenitors of a numerous and varied offspring. The chief of these are the genera *Elodina* and *Nychitona*, the former of which is entirely confined to the Australian Region, while the latter has a very wide distribution throughout the Ethiopian, Oriental, and Australian. The African

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* I here follow Mr. Sclater's division of the earth's surface into six Zoological Regions, which arrangement, adopted by Mr. Wallace in his "Geographical Distribution of Animals," 1876, has stood the test of time and experience better, in my opinion, than any alternative distribution that has been proposed. I also adopt, for convenience, the smaller divisions, or "sub-regions," as determined by Mr. Wallace in the above-named work.

species of *Mylothris* belong possibly to the same category.

The genera derived from the *Catasticta* group remain, for the most part, within the confines of the Neotropical Region. This is the case with *Pieris, Leptophobia, Hesperocharis,* the American species of *Mylothris,** *Dismorphia, Moschoneura,* and those species allied to *monuste* at present included in the genus *Udaiana.*† It is remarkable that the Nearctic Region does not furnish a single species that can be supposed to be derived from the present stem.‡ Inasmuch, however, as the Palæarctic genus *Leptosia* seems to belong rather to this than to any Eastern branch, the conjecture may be hazarded that connecting forms now extinct once occupied the Nearctic Region, from which the Palæarctic continent received the forerunners of its present *Leptosias,* probably by way of Behring Strait.

Turning now to the Eastern *Metaporia,* which inhabits the borderland between the Palæarctic and Oriental Regions, we find it emitting one clearly-defined branch in the Palæarctic direction. This is the branch to which belong the various species of *Pontia,* as *P. nabellica, P. soracta, P. hippia, P. belucha, P. leucodice,* and *P. cratægi.* In the Chilian or Andesian division of the Neotropical Region we find the genus *Tatochila,* which appears not to belong to the regular Neotropical Pierine stock, but to be closely related to the Palæarctic *Pontias.* It is conceivable that the latter stem may have spread from Asia into the western portion of the Nearctic continent, and thence down the mountain-chains to the south. *Neophasia menapia,* at present inhabiting the Californian and Rocky Mountain sub-regions, seems to me to be more nearly allied to both *Pontia* and *Tatochila* than (as Behr thinks) to *Eucheira socialis,* and may very possibly be a relic of the original invasion. Another indication of the same invasion is afforded by the genus *Phulia,* now found with the nearly-allied *Tatochila* only in the Andesian or Chilian

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* See p. 320, note.

† See p. 321.

‡ The instance of *U. monuste,* which straggles into the southern districts of the Nearctic Region, hardly forms an exception to the above statement.

sub-region, to which it no doubt made its way along the great mountain-chains in a similar manner. Its close ally, *Baltia*, remains in the high lands of Central Asia, where it bears much the same relation to *Synchloe* as *Phulia* to *Tatochila*. Another early offshoot from the Eastern *Pontia* stem is *Mesapia peloria*,* which has no representative in the Western Hemisphere.

The above descendants of the mountain *Metaporias* belong, as has been seen, in the first place, to the Palæarctic and western portion of the Nearctic Region, only reaching the Neotropical by extension along the chain of the Andes. Other derivatives of *Metaporia*, however, took their course directly southwards. The first of these is the *Delias* and *Prioneris* group, the more ancient members of which are, speaking generally, to be found in the northern portion of the Indian peninsula, while the Australian and other southern forms represent, as a rule, a somewhat later stage of development. Another is the important branch headed by *Huphina*, which genus, like *Delias*, has spread downwards throughout the Oriental Region, and by way of the Indo-Malayan and Austro-Malayan islands to the Australian continent. The Australian species of *Huphina* are clearly derived from the Oriental, and those forms (such as *H. phryne* ♀) which are nearest to *M. agathon* in colouring are also its closest neighbours geographically. Of the two genera (*Hiposcritia* and *Catophaga*) which appear to be immediately derived from *Huphina*, the former is confined to the Oriental Region; while the latter, like *Huphina* itself, has spread along the Austro-Malayan Islands to the Australian mainland. This is also the case with *Appias*,† the origin of which genus from the *Catophaga* stock is no doubt to be assigned to the Oriental Region. But, unlike the other genera, *Appias* seems to have extended its borders westwards, and to have given rise to the "*Phrissura B*"‡ group in the Ethiopian Region, and even to *Glutophrissa* in the Neotropical. If this be the real origin of these two latter genera, we have to enquire how they reached the African and South American continents respectively.

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* See p. 304.

† It would seem, however, that no true *Appias* actually reaches the Australian continent.

‡ See p. 309, note.

With regard to the first, there is little difficulty in supposing the passage to have been effected by land either now or formerly existing, the Ethiopian Region having been in this, as in so many other instances, first entered from the north. But it is not easy with our present knowledge to imagine an overland passage for these butterflies from the Oriental or Ethiopian Region to the Neotropical. The northward route, which we saw to be the one probably adopted by the ancestors of the Chilian *Phulias* and *Tatochilas* in spreading from Central Asia, is excluded in the present instance by the entire absence of any trace of such a passage from both the Palæarctic and Nearctic Regions; and although a transit by way of a formerly existing *"* Antarctica*"* is conceivable, it would seem more likely that the crossing from east to west was effected in the region of the tropics. After all, however, the difficulty of supposing an Atlantic sea-passage is not overwhelmingly great. The unusual facilities possessed by insects for crossing large extents of sea have been remarked by many writers,* and among insects the butterflies of the Pierine group are especially given to migration for great distances in countless hordes.† It is worth noting that in the case of each of the other three chief Pierine genera whose present distribution seems to have involved one or more long sea-passages, *i.e.*, *Terias*, *Colias*, and *Callidryas*, special observations exist of their migratory propensities. In 1874 a large swarm of *Terias lisa* reached the Bermudas from the American continent;‡ the swarm of butterflies described in a well-known passage|| by Mr. Darwin consisted chiefly of a species of *Colias*; while descriptions of the migratory flight of *Catopsilia* and *Callidryas* are numerous, among the most striking pieces of testimony being that

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* See especially Wallace's "Geographical Distribution," 1876, vol. i., p. 32; and the same author's "Darwinism," 1889, p. 359, etc.

† Trimen, Trans. Ent. Soc. Lond., 1870, p. 382; "South-African Butterflies," 1887, vol. iii., p. 32. Moore, "Lepidoptera of Ceylon," 1880, 81, p. 116. Distant, "Rhopalocera Malayana," 1882—86, p. 285, etc. Mr. Trimen suggests that there is "an evident connection or relation between these wonderful migrations of certain species of *Pierinæ* and the well-known habit of nearly all the members of the Sub-family of flying straight onward in one direction."

‡ "Psyche," Dec. 1875, p. 121.

|| "Voyage of the Beagle," ed. 1860, p. 158.

of Mr. Spruce, who saw *Callidryas* "launching boldly out over the Pacific Ocean."*

The earliest species of *Synchloe* were undoubtedly differentiated from *Pontia* or *Baltia* in the Palæarctic Region, from which the genus spread (probably eastwards) into the Nearctic. *Synchloe* proper can hardly be said to enter the Indian Region,† but in its progress westwards it has sent an offshoot downwards into the Ethiopian, consisting of *S. johnstonii* and *S. hellica*. *S. glauconome* of Arabia and Egypt remains to mark the course of the invasion. *Ganoris*, a further Palæarctic development of *Synchloe*, has accompanied that genus into the Nearctic Region and has also spread into the Oriental. A curious extension of the range of the Palæarctic *G. rapæ* into the Nearctic Region has been in progress during the last thirty-three years, the first transatlantic specimens having been seen at Quebec in the year 1860.‡ This introduction was undoubtedly effected by human agency, and differs from the natural passage of species between the two Regions in having taken place by the Atlantic instead of the Pacific route.

Though *Synchloe* itself is far more characteristic of temperate than of tropical districts, it has given rise to a large and important Pierine branch which has spread far and wide through tropical and temperate parts alike. The birthplace of *Herpænia* and *Teracolus*, the two earliest members of this extensive section, is apparently the eastern portion of the Mediterranean division of the Palæarctic Region; from which locality the former has spread through Arabia and Abyssinia into the African continent, while the latter has not only followed *Herpænia* into Africa, but has also largely occupied the two western Oriental sub-regions. Those forms of the genus *Ixias* that show least divergence from *Teracolus* are found in the Nile provinces of Eastern Africa, but the bulk of this genus has moved eastwards, its distribution being characteristically Indian. A few species, however, are found in some of the Indo-Malayan islands, and in Austro-Malaya as far east as Timor.

* Journal Linn. Soc., Zool., ix., pp. 355—357.

† See Wallace, Trans. Ent. Soc. Lond., 3rd series, iv., pp. 242, 3.

‡ Scudder, "Butterflies of the Eastern United States," 1889, vol. ii., pp. 1175-1190; Edwards, "Butterflies of North America," vol. i., 1868-72, *sub. voc. P. virginiensis*.

To the same borderland of Western Asia and Eastern Africa may be assigned the place of origin of *Nepheronia*, which has sent a western branch into Africa, and an eastern into the Indian peninsula and Malayan islands, one species reaching the Australian continent. The African branch has given rise to *Eronia* proper. Attention has already been drawn to the curious fact that the form which links the *Eronia* group most closely with *Teracolus*, viz., *E.* (?) *lucasii*, survives in Madagascar. *Hebomoia*, another offshoot of this part of the Pierine stock, is now almost entirely Malayan; its place of origin was, however, in all probability further west. The birthplace of *Euchloe* is problematical, but the present distribution of the *charlonia* group, which seems to contain the oldest members of the genus, would appear to make it probable that the Mediterranean sub-region witnessed the rise of this, as of so many other more or less direct descendants of *Synchloe*, from which central area it successively overspread the Palæarctic and Nearctic continents. The isolated geographical position of *Eroessa chilensis* is very remarkable, its affinities being apparently with Eastern rather than Western forms. It is probably, as before suggested, a solitary survival of a once more widely-spread group, among which were to be found the immediate ancestors of the present-day *Euchloes*.

No other genus in the whole sub-family has so extensive a range as *Colias*, species of which are found in every one of the six great Zoological Regions. Here again, I have little doubt that the site of original divergence is Asiatic, and is most nearly represented in the present condition of the earth's surface by the borderland between the Palæarctic and Oriental Regions on the north-west frontier of India. From this centre one or two species have ranged into South Africa and the Indian peninsula ; but the greater number have turned northwards, and after populating the Palæarctic and Nearctic continents with numerous species, have penetrated to the circumpolar lands within the Arctic Circle, have passed down the great mountain chains of Central and South America to Chili and Patagonia, and have even established outposts in Venezuela and the Sandwich Islands.*

The powers of dispersal possessed by the genus *Terias*

* The occurrence of *Colias* in the last-named locality is, however, not entirely free from doubt.

are almost as remarkable as those of *Colias*; perhaps even more so when we take into account their weak flight, and the fact that their migrations must have been intertropical. Mr. Wallace, however, has drawn attention to their habit of frequenting "gardens and plantations and skirts of forests rather than their deeper recesses," and also of "assembling on the margins of streams and on the sea beach," and has remarked that "these habits lead to their being frequently carried off by winds," and that "it is thus perhaps that some of the species have so wide a range and offer such perplexing variations."* Whatever may have been their means of dispersal, there can, I think, be no doubt that they took their rise from the *Colias* stock in the Western Hemisphere, the line of descent passing through *Xanthidia* to *Terias* and *Sphænogona*; *Pyrisitia, Nathalis,* and *Leucidea* being given off by the way. All these genera are mainly Neotropical with Nearctic extensions. *Terias* itself, however, as is well known, so far from remaining within these limits, has overspread the warmer portions of the Ethiopian, Oriental, and Australian Regions, and is even found in the Manchurian sub-region of the Palæarctic.

It seems on the whole most probable that the origin of *Gonepteryx* is also to be referred to the Western Hemisphere, where *Meganostoma* marks the transition from *Colias*. *Gonepteryx* itself seems to have passed to the north by way of California and so across into the Palæarctic Region, while *Rhodocera* and *Amynthia* represent a Neotropical development of the same stock, the Central American genus *Kricogonia* perhaps remaining near the original seat of divergence. *Gonepteryx* having reached the Palæarctic Region has extended to its westernmost extremity. Its only offshoot appears to be *Dercas,* which probably arose in the debateable Manchurian area, where the Palæarctic and Oriental faunas are much mixed, and thence spread southwards through the Indo-Chinese sub-region to Sumatra and Borneo.

Catopsilia and *Callidryas,* like *Terias,* must, it would seem, have undergone intertropical migration. Their oldest forms appear to be *Catopsilia florella, C. hyblæa,*

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* Trans. Ent. Soc. Lond., 3rd series, iv., p. 320. See also above, p. 325.

C. thauruma, etc., which are probably derived from the Neotropical genus *Amynthia,* coming nearest to *A. clorinde.* Inasmuch as all these are African insects, and the New World *Callidryas, Phœbis,* and *Metura* are less closely allied to *Amynthia,* it seems necessary to suppose that the earliest forms of this group in the Neotropical Region have become extinct, the present *Callidryas* group surviving as their modified descendants; while an early dispersal of these ancestral forms took place across the Atlantic to Africa, of which invasion *C. florella,* etc., remain as comparatively unmodified relics. The Oriental and Australian *Catopsilias* are the ultimate developments of this invasion.

The distribution of *Belenois* is remarkable, the bulk of the species belonging to the Ethiopian and Australian Regions. The Oriental Region is poorly supplied, except for the abundant *B. mesentina,* which is found in all parts of the Indian peninsula, and even enters the Mediterranean district of the Palæarctic Region as far as Asia Minor. Notwithstanding the present poverty of the Oriental Region in species of *Belenois,* it seems probable that this area is really the birthplace of the genus, which, as we have seen, appears to be derived from that primitive part of the Pierine stem now represented by *Delias* and *Prioneris.* *B. mesentina* and *B. taprobana,* of India and Ceylon, may probably be regarded as survivors of the original race of *Belenois,* whose descendants have spread south-eastwards to Australia, and south-westwards to Madagascar and the African continent. *Pinacopteryx* is in all probability a local modification of *Belenois* within the Ethiopian Region, while *Daptonura,* whose history is otherwise hard to account for, may perhaps have originated from a branch of the African *Belenois* which at some remote period found its way westwards across the Atlantic.

In concluding this paper I wish to express my great indebtedness to several friends who have given me valuable help during its progress. It was by the kindness of the late Professor Westwood that I was enabled to begin the study of the Pierine group in the Hope Collection at Oxford, and the facilities for work afforded me by him have been continued and increased by his successors in the charge of the department, first by

Mr. W. Hatchett Jackson, and now, in a special manner, by Professor Poulton, F.R.S., the present occupant of the Hope Chair, at whose request I have undertaken the arrangement of this part of the Hope Collection. I am also under great obligations to Colonel Swinhoe, who has very kindly helped me in various ways, and especially in the determination of the Eastern species, of which he has so intimate a knowledge. Lastly, my thanks are due to the members of the staff of the Natural History Department of the British Museum, particularly to Messrs. A. G. Butler, W. F. Kirby, and F. A. Heron, who have given me every assistance in examining the fine series of *Pierinæ* preserved in the National Collection.

IV.—Index of Species Mentioned.

The Order is that of the National Collection in the British Museum.

Pierinæ.

* Probably not a *Mylothris*; see Trimen, "South-African Butterflies," vol. iii., 1889, p. 35, note.

Danainæ.

Heliconinæ.

EXPLANATION OF PLATES III., IV., & V.

PLATE III.

FIG. 1. *Eucheira socialis.*
2. *Catasticta bithys.*
3. *C. ctemene.*
4. *Delias belladonna.*
5. *D. eucharis* ♀.
6. *D. nysa* ♂.
7. *Metaporia agathon.*
8. *Huphina phryne* ♀.

PLATE IV.

FIG. 9. *Catophaga paulina* ♀.
10. *Appias clementina* ♀.
11. *Hiposcritia lalage* ♂.
12. *Mylothris agathina.*
13. *Belenois mesentina* ♂.
14. *B. peristhene.*
15. *Synchloe daplidice* ♀.
16. *Ganoris napi* ♀.

PLATE V.

FIG. 17. *Teracolus hewitsonii.*
18. *Ixias marianne* ♀.
19. *Hebomoia glaucippe* ♀.
20. *Colias hyale* ♀.
21. *Catopsilia crocale,* var. *flava* ♀.
22. *Callidryas philea* ♀.*
23. *Eronia leda* ♀.
24. *Euchloe charlonia.*

These figures are only designed to illustrate the actual points mentioned in the text. They are not intended to show specific characters. The same letters and numbers stand for the corresponding markings throughout all the figures. See explanations in the text, pp. 254, 264, 269, 273, 274.

NOTE.—In Fig. 15, S 8 is placed one space too high up.

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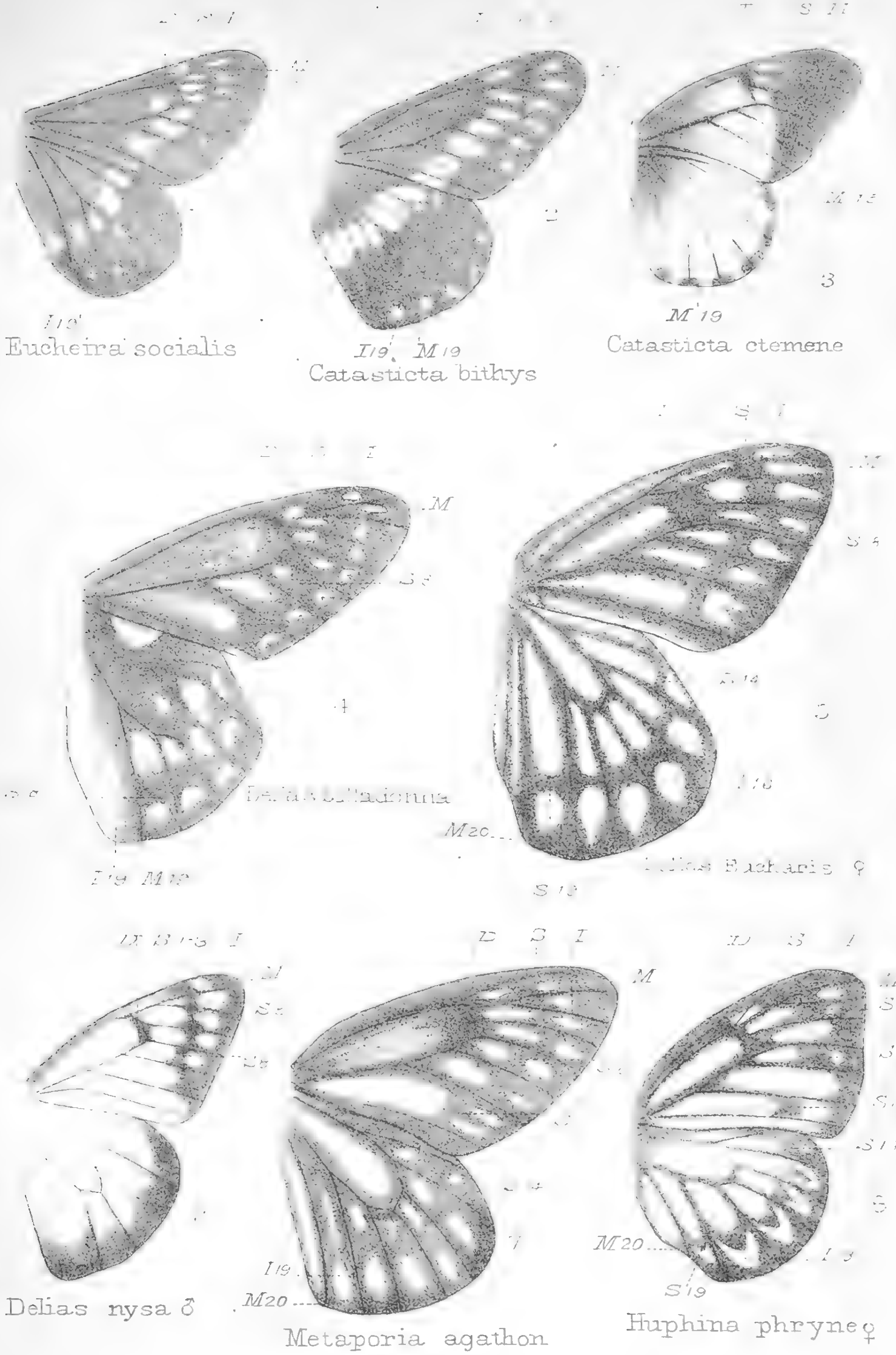
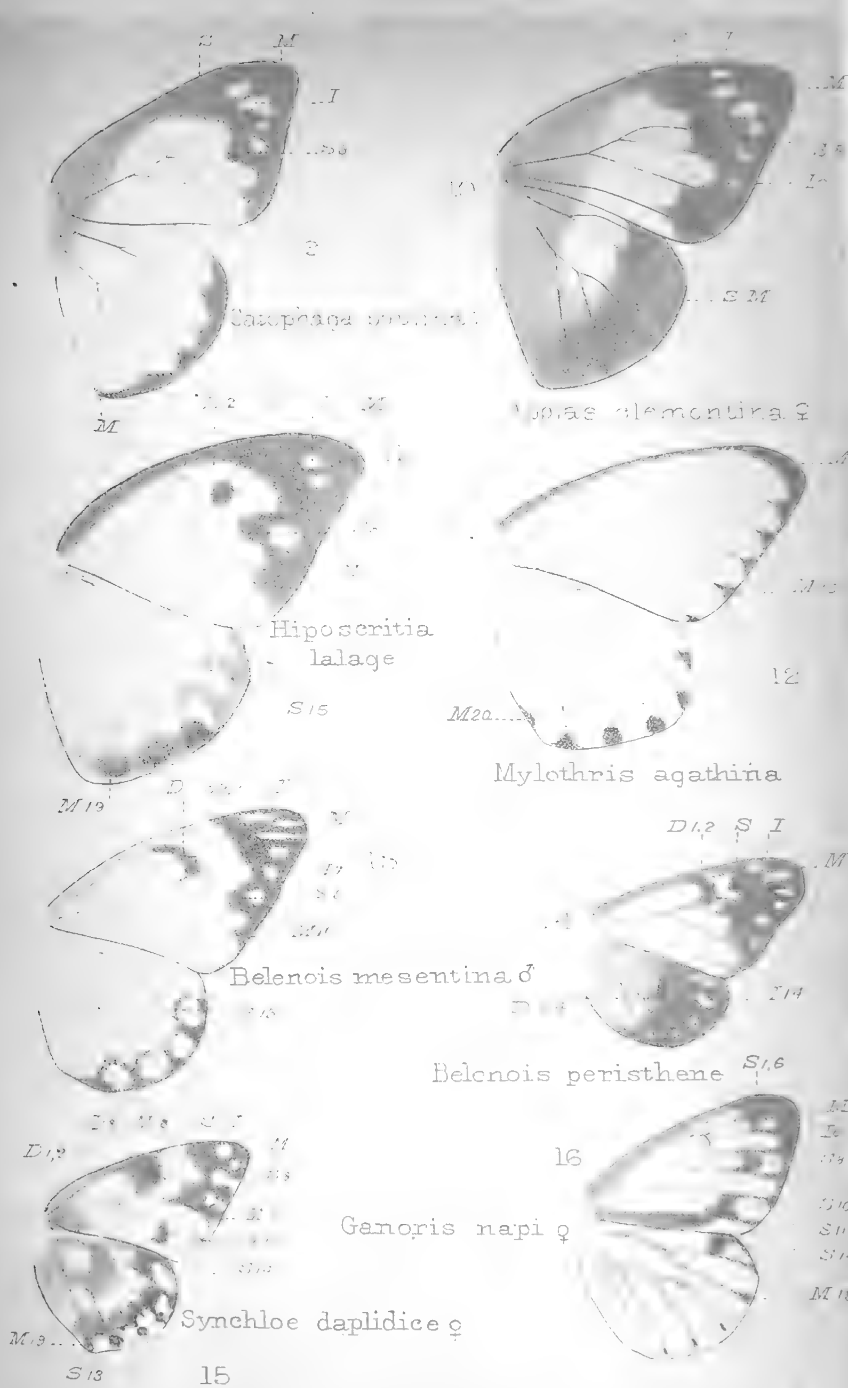
* This figure was drawn from a specimen in the Hope Collection, which had been erroneously labelled *C. thalestris.* The error has unfortunately found its way into the plate.



F. A. Dixey del.

West, Newman lith.

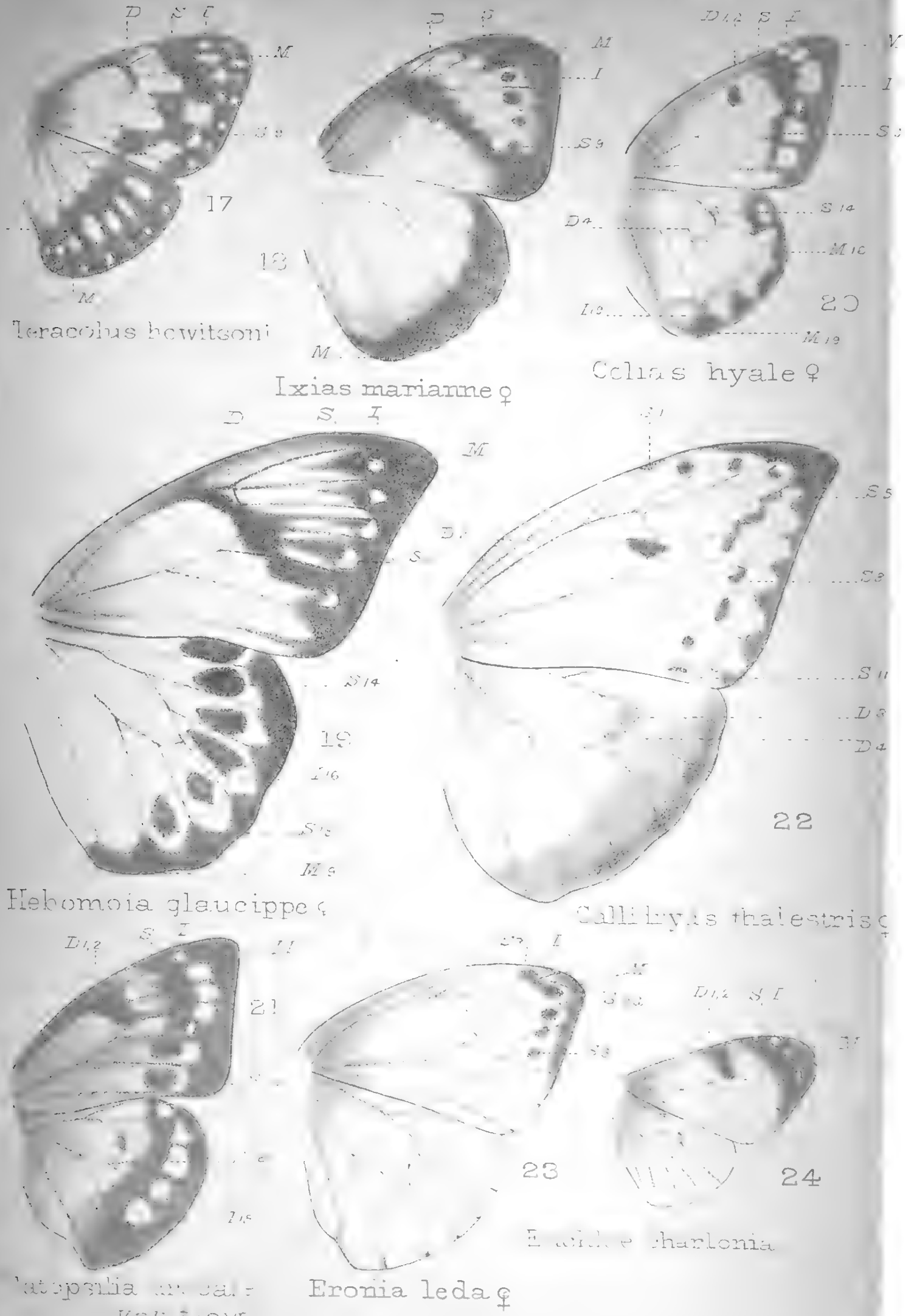
Wings of Pierinæ.



F. A. Dixey del.

West, Newman lith.

Wings of Pierinæ.



F.A. Dixey del.

West, Newman lith.

Wings of Pierinæ.

ON

WALKER'S AMERICAN TYPES

OF

LEPIDOPTERA

IN THE

OXFORD UNIVERSITY MUSEUM.

BY

W. SCHAUS, F.Z.S.

[*From the* PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON,
June 16, 1896.]

On Walker's American Types of Lepidoptera in the Oxford University Museum. By W. Schaus, F.Z.S.

The following notes on Walker's American types in the Oxford University Museum are to be followed by others, wherein the complete synonymy will be given of many of the species, and references will also be made to those species which as yet remain unidentified. My special thanks are due to Prof. E. B. Poulton, F.R.S., for the trouble he took in selecting the American Moths from the Hope Collection, and sending them family by family to the British Museum to be compared with the collections there and with my own collection; and to Mr. G. F. Hampson for his untiring kindness and assistance. Those species marked with an asterisk are represented in my own collection; those of which I do not possess specimens, and which are not in the British Museum either, have been figured in duplicate, one set of figures being placed in the Entomological Department of that Museum. The species described by Walker in parts 27–30 of his Catalogue, and in the corresponding portions of the Supplement, as being in "Coll. Saunders" never formed part of the Hope Collection of the Oxford Museum, but have lately been purchased by the British Museum, where the types are now to be found.

The references given refer to Walker's 'List of the Specimens of Lepidopterous Insects in the Collection of the British Museum.'

Vol. III.

P. 775. **Norape puella* described from the Fry coll. is now in the Saunders coll., and is the same as *Archylus pectoralis*, Walk.

Vol. IV.

P. 801. *Sarsina purpurascens*. I have not yet been able to find the type.

P. 895. **Darala falcata*=*Lonomia submacula*, Walk.

P. 957. *Isychagrapha floccosa*. Not identified.

Vol. V.

P. 1046. **Naprepa camelinerdes* is a distinct species belonging to the Notodontidæ.

P. 1115. *Laruma heterogenea* is a distinct species, the genus being the same as *Hydrias*.

P. 1152. *Nesara apicalis* belongs to the genus *Ocha*, Walk.

P. 1155. **Pamea excavata* and *Pamea notata* are the sexes of one species.

P. 1155. **Pamea vittata* belongs to the genus *Carthara*, Walk.

P. 1170. *Rosema deolis* is not Cramer's species, and I therefore propose the name of *R. walkeri* for it; the species is well described by Walker.

Vol. V. (*continued*).

P. 1176. **Tepilia biluna* is the same as *Phecada confinis*, Walk.

P. 1195. **Lonomia albigutta* is a well-known species, but will no doubt sink as a synonym of one of Cramer's species.

Vol. VI.

P. 1264. *Tropæa dictynna*. Evidently a distinct species and not a mere var. of *T. luna*.

P. 1300. **Hyperchiria memusæ*. A good species allied to *H. leucane*, Hbn.

P. 1301. **Hyperchiria cinerea*. The ♀ of *H. janeira*, Westwood.

P. 1301. *Hyperchiria pyrrhomelas* is a good species.

P. 1303. **Hyperchiria submacula* has been redescribed by Boisduval as *H. dioxippus*.

P. 1313. **Hyperchiria vagans* is a species of *Dirphia*.

P. 1326. *Rhescynthis meander*. This is well figured by Maassen and Weymer.

P. 1329. **Dysdæmonia glaucescens*. A distinct species.

P. 1338. *Mimallo plana* belongs to the genus *Perophora*.

P. 1364. **Dirphia multicolor* is a distinct and well-known species.

P. 1402. **Hydrias albidifascia*. A distinct species.

P. 1402. **Hydrias plana*. A distinct species.

P. 1403. *Hydrias confusa*. The type is the only specimen I have seen of this species.

P. 1507. *Hydrias tenebrosa*. Not identified.

Vol. VII.

P. 1598. *Seryda cincta*. Not identified.

P. 1601. *Pseudomya consolata* belongs to the genus *Læmocharis*.

P. 1602. *Pseudomya desperata*. Closely allied to *P. tipulina*, Hübn.

P. 1602. *Gymnelia bijuncta*. Subsequently described by Walker as *G. consociata*.

P. 1603. *Gymnelia simplex*. A distinct species.

P. 1603. **Gymnelia xanthocera*. A distinct species.

P. 1604. *Isanthrene odyneroides* is a species of *Erruca*.

P. 1606. *Pœcilosoma sperans* belongs to the genus *Marissa*.

P. 1606. *Pœcilosoma insperata* also belongs to the genus *Marissa*.

P. 1607. *Pœcilosoma gaudens* belongs to the genus *Dycladia*.

P. 1608. **Lagaria acuminata*. Redescribed and figured by Schaus in Lep. Am. as *Gartha dalsa*.

P. 1609. *Læmocharis contracta* belongs to the genus *Erruca*.

P. 1610. *Ilipa tenthredoides*. Also in B. M.

P. 1611. *Ilipa scita*=*S. hilaris*, Walk., in B. M.

P. 1613. *Cosmosoma marginatum* is a distinct species.

P. 1615. **Eurata transiens*=*Dycladia lucetius*, Cr.

P. 1617. **Eunomia vacillans* is a good species.

P. 1617. **Eunomia abdominalis*=*Corematura chrysogastra*, Perty.

P. 1618. *Eunomia separata*. Not identified.

P. 1619. *Pseudosphex consobrina*. Also in B. M.

P. 1619. *Pseudosphex cognata*=*Ps. fasciolata*, Butl., in B. M.

P. 1620. *Myrmecopsis opaca*=*Ps. vespa*, H.-S., fig. 426.

VOL. VII. (*continued*).

P. 1627. *Calonota perspicua.* A distinct species.
P. 1628. *Calonota interrupta.* Allied to the preceding.
P. 1629. **Pampa acuminata.* Redescribed and figured by Schaus in Lep. Am. as *Sychesia hartmanni.*
P. 1629. *Pampa fusiformis* = *Scepsis trifasciata*, Butl., in B. M.
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P. 1400. **Botys cellatalis*=*Acharana phæopteralis*, Gn.
P. 1466. **Scopula permixtalis* belongs to the genus *Phlyctænia*.
P. 1492. *Bouchis scoparioides* belongs to the genus *Ethnistis*.
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P. 1702. *Lephana tetraphorella* belongs to the Noctuidæ. Type in B. M.
P. 1743. *Gabalæca bilineatella* belongs to the genus *Erupa*. Type in B. M.
P. 1769. *Zolca congruella* belongs to the genus *Erupa*. Type in B. M.
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P. 1800. *Torda metamelana*=*Tosale pyralidoides*, Walk. Type in B. M.
P. 1958. *Celæna canifimbria* belongs to the Noctuidæ. Type in B. M.
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P. 101. **Asthana directa* belongs to the genus *Pœsula.*
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P. 104. **Remigia consistens*=*Renodes brevipalpis*, Gn.
P. 104. *Gangra atripustula* belongs to the Thermesiidæ.
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P. 108. **Marthama conspersa*=*M. squamivaria*, Walk.
P. 109. **Hypena murina*=*H. exoletalis*, Gn., in B. M.
P. 115. **Bocana marginalis*=*B. orionalis* ♂, Walk.
P. 122. *Salbia varialis* belongs to the genus *Phostria.* In B. M.
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P. 126. *Scopula desistalis* belongs to the genus *Ebulea.*
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P. 260. *Poaphila plagiata.* Not identified.
P. 260. *Poaphila figurata.* Not identified.
P. 260. *Phurys mensurata.* Not identified.
P. 260. **Hypena scissilinea* belongs to the genus *Saserna* and is well figured in the Biol. Centr.-Amer.
P. 271. *Rhagonis bicolor.* Not identified.
P 277. **Pœcilocampa plurilinea*=*Tolype opalina*, Walk.

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Contributions to Marine Bionomics.

By

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I. The Habits and Respiratory Mechanism of Corystes cassivelaunus.

Corystes cassivelaunus is a crab of unusually narrow and elongated form, which has received the popular name of "masked crab" from the grotesque resemblance which its sculptured carapace bears to a human face. It is common round all the coasts of the British Isles, and, although normally an inhabitant of the deeper water, is occasionally found at home in sandy pools on the sea shore, and is frequently cast up in hundreds on sandy shores after heavy gales.

I. Systematic Position.

The systematic position of the Corystoidea has long been a disputed point among carcinologists. Henri M. Edwards (1834) placed the Corystoid crabs near the Dorippidæ among the Oxystomata, and regarded them as connecting links between the Cancroidea (*viâ* the Calappidæ) on the one hand, and the Anomoura on the other.

De Haan (1849) removed the family from the group Oxystomata altogether, and placed it with the Cyclometopa and Catometopa of M. Edwards, in a separate sub-division of the Brachyura, the Brachygnatha.

Dana (1852) made of the Corystoidea an independent and primary tribe of the Brachyura, distinct from the Cancroidea and Leucosoidea alike.

Alphonse Milne-Edwards (1860) reverted to the older view, and placed the Corystidæ near the Calappoid Oxystomata. Heller also (1863) placed the Corystidæ among the Oxystomata.

Finally, Claus (1880) definitely placed the Corystidæ in the Cyclometopa. In this he has been followed by Miers (1886) and Stebbing (1893).

It cannot be said, however, that the real position and affinities of the Corystidæ are yet established. The reason for this uncertainty is probably due to the fact that, as will appear further on, the structure of these animals is remarkably modified in relation to sand-burrowing habits. Some of these adaptive modifications of structure, which reappear in certain other groups of Crustacea, have undoubtedly impressed the minds of certain writers with ideas of homology and genetic relationship between the Corystidæ and groups having no real affinity with that family. The case affords a new illustration of the inadequacy of the purely morphographic method, when unchecked by considerations of functional adaptation, for the solution of problems of relationship and genetic classification.

II. Structural Peculiarities.

The structure of *Corystes cassivelaunus* is noteworthy on account of the following features. The second antennæ are greatly elongated—as long as, or longer than, the body—and are fringed along their entire length by two rows of hairs, one of which runs along the ventral, while the other runs along the dorsal border of the antenna. The hairs of each row curve inwards towards those of the corresponding row on the second antenna of the opposite side. The second antennæ shew a marked tendency to approximate to one another longitudinally; the opposing rows of hairs then interlock, with the resulting formation of a median tube, the lateral walls of which are formed by the jointed flagella of the antennæ, while the dorsal and ventral walls are fenestrated along their whole extent by the interspaces between the interlocking hairs. The organ formed by the apposition of the second antennæ I shall term the "antennal tube."

The long axes of the three stout basal joints of the second antenna are disposed at right angles to one another, and bring about a characteristic double bend in the basal part of the antenna. The double row of hairs found on the flagellum of the antenna is continued backwards along these three basal joints. The hairs on the most distal of the three joints interlock with those of the corresponding joint of the opposite antenna; the hairs on the anterior face of the deflected middle joints bend inwards towards the median line along the sides of the rostrum, and together with a median triangular tuft of hairs springing from the rostrum itself, form the hairy roof of the proximal part of the antennal tube.

The antennal tube opens posteriorly into a rectangular chamber in front of the mouth. This "prostomial chamber," as it may be termed, is roofed by the rostrum in front, the antennal and epistomial sternites

in the middle, and the prelabial plate behind. It is flanked by the two basal joints of the second antennæ in front, and by a forward process of the pterygostomial region of the carapace behind. Its floor is imperfect, and is formed by the anterior part of the third maxillipeds behind, and by a quadrangular sieve in front, furnished by the hairs springing from the two basal joints of the second antennæ, the anterior pterygostomial processes, and a special anterior process of the fourth joint of the external maxillipeds. The hairs from all these parts are directed inwards towards the centre of the quadrangular space outlined by the boundaries of the prostomial chamber, and constitute a complete sieve-like floor to the chamber in question. On each side this prostomial chamber leads by a wide aperture into the branchial cavity.

The participation of the epistome together with the prelabial space in the formation of a prostomial chamber is one of the features which strongly distinguishes the Corystoid crabs from typical Cyclometopa, Catometopa, and Oxyrhyncha. The arrangements of these parts approximates in some respects to that found in the Oxystomata, where the buccal frame or the peristome is prolonged anteriorly as a definite prostomial chamber to the very tip of the snout. This chamber in the Oxystomata, however, is completely closed in by the third maxillipeds, and is very narrow anteriorly; in the Corystoidea, on the other hand, it is broad in front, and is imperfectly closed by the third maxillipeds.

III. Previous Observations on Habits.

In Bell's "British Stalk-Eyed Crustacea" (1853) a brief reference is made to the sand-burrowing habits of *Corystes cassivelaunus.* Couch had already described the crab as "burrowing in the sand, leaving the extremities of its antennæ alone projecting above the surface." The actual process of burrowing appears not to have been observed at the time when Bell wrote, for he quotes Couch's suggestion that the elongated antennæ possibly "assist in the process of excavation." This theory of the function of the antennæ was subsequently rejected by Gosse (1865), as a result of his own observations on the habits of the crab, and again by Hunt (1885), who correctly states that the crab descends into the sand backwards with the greatest agility, "thus leaving the antennæ no opportunity of assisting in the operation."

The first writers to offer anything approaching a real explanation of the use of the antennæ were the veteran naturalist of Cumbrae, Mr. David Robertson, and Mr. P. H. Gosse. It is difficult to say, and would indeed be ungenerous to enquire, which of these two naturalists has the priority in the matter. Gosse, in 1855, described the outer antennæ of *Corystes* as "together forming a tube" (*Manual of Marine*

Zoology, I., p. 158), but he did not apparently publish his observations in full until 1865.

In the meantime Mr. David Robertson communicated to the Philosophical Society of Glasgow, on March 13th, 1861, an interesting note on the function of these antennæ. He described the burrowing habits of the crab, and shewed that, under these circumstances, the antennal tube preserved "a free passage for the purpose of enabling the animal to carry on the process of its aqueous respiration." Mr. Robertson believed, with Gosse, that the current through the tube was exhalent in character. In another paper he stated that "he had seen the ova cast up through the opening [of the antennal tube]—the inference being that the animal had placed it by means of its claws within the influence of the current." (*Proc. Nat. Hist. Soc., Glasgow*, vol. i. p. 1.)

Gosse (1865) similarly observed that each antenna, from the form and arrangement of its bristles, constituted a "semi-tube, so that when the pair was brought face to face the tube was complete." He also carefully watched a living specimen, as it was sitting upright on the top of the sand, close to the side of a glass aquarium, and observed that the antennal tube formed a channel for a definite current of water. To quote his own words: "I immediately saw that a strong current of water was continuously pouring up from the points of the approximated antennæ. Tracing this to its origin, it became evident that it was produced by the rapid vibration of the foot-jaws, drawing in the surrounding water, and pouring it off upwards between the united antennæ, as through a long tube. . . ." "I think, then, that we may, with an approach to certainty, conclude that the long antennæ are intended to keep a passage open through the sand, from the bottom of the burrow to the superincumbent water, rendered effete by having bathed the gills; and it is one of those exquisite contrivances and appropriations of structure to habit which are so constantly exciting our admiration . . . [and] are ever rewarding the research of the patient observer."

We shall see below that while Gosse's conduit-theory of the function of the antennæ is perfectly correct, his inferences as to the function of the antennal conduit are true only to a limited extent. Gosse assumed that the habits of the crab when beneath the sand were similar to its habits when above the sand, and confined his observations to the crab in the latter condition. Experiment shews, however, that there may be a marked difference in the working of certain organs under the different conditions.

A third theory as to the function of the antennæ in *Corystes cassivelaunus* is due to Mr. A. R. Hunt (1885). He says, "I incline to think that the function of the antennæ is to maintain a communication between the buried crab and the water above, as without some such con-

nexion there would be a risk of the animals being occasionally buried to a dangerous depth by the accumulation of sand above them. Mr. W. Thompson's statement that the antennæ in very small specimens are much longer in proportion to the carapace than in the adult harmonizes well with this hypothesis, as to ensure safety the young would have to burrow to a greater depth compared with the adults than would be proportionate to their size." Mr. Hunt was not aware of Gosse's view when he framed the above theory; but, subsequently, in a footnote to his paper, he referred to Gosse's theory as identical with his own. The two are, however, essentially distinct, if I correctly understand Mr. Hunt's language. According to Gosse's view, the function of the antennæ is to produce a tube subservient to respiration; according to Mr. Hunt's, the function of the elongated antennæ is essentially sensory, viz., to enable the buried crab to determine the depth to which it burrows. The "danger" to which Mr. Hunt refers is clearly not the danger of suffocation, but the danger of dislodgment from the sand by wave-currents. The arenicolous habits of *Corystes* are adduced by Mr. Hunt to illustrate one of the various methods adopted by marine animals for resisting wave currents—a view which, in the case of *Corystes*, I am unable to accept, partly on account of the normally deep water habitat of the crab, and partly on account of evidence given below which tends to shew that the burrowing habits of *Corystes* are adopted primarily for concealment.

IV. New Observations and Experiments.

(a) Burrowing Habits. A number of living *Corystes cassivelaunus* were placed in a series of vessels containing sand of different degrees of coarseness, and it was soon noticeable that these crabs readily burrow in fine sand, but find great difficulty in penetrating very coarse sand or gravel composed of small pebbles. Moreover, a crab that has obstinately declined for several hours to burrow in coarse, gravelly sand, will immediately bury itself, if placed in an aquarium of fine sand. In all cases the process of burrowing is effected exclusively by means of the thoracic legs. The crab sits upright on the surface of the sand; the elongated, talon-like claws of the four hindmost pairs of legs dig deeply into the sand; the body of the crab is thus forcibly pulled downwards by the grip of the legs, and the displaced sand is forced upwards on the ventral side of the body by the successive diggings and scoopings of the legs; the slender chelate arms of the first thoracic pair assist in the process of excavation by thrusting outwards the sand which accumulates round the buccal region of the descending crab. This action at the same time, no doubt, loosens the sand in the immediate neighbourhood, and

renders easier and quicker the descent of the crab into its sandy burrow. Briefly stated, in fact, the four hindmost pairs of legs are all engaged in pulling the crab downwards, while the first or chelate pair is engaged in pushing away the more superficial sand in the neighbourhood of the crab's maxillipeds. The two actions combine to drive the crab downwards and obliquely backwards. The main object of this latter motion appears to be the prevention of any forcible intrusion of sand into the buccal apparatus.

When the carapace of the crab has completely disappeared beneath the surface of the sand, the antennæ are frequently seen to be rubbed obliquely against one another for two or three strokes, whereby the hairs on the antennæ are cleansed from adhering particles. This very characteristic action of the antennæ was noticed long ago by Couch, and correctly recognised by him as a process of cleansing (*vide* Bell, p. 161). After this cleansing process, however, the crab proceeds still further in its act of burrowing, and descends deeper and deeper until nothing is visible above the sand but the most distal portion of the antennal tube.

Resting passively in its bed of sand, *Corystes cassivelaunus* spends the daytime thus concealed from all observation. In aquaria an individual will occasionally emerge and remain on the surface of the sand for some time, but this can usually be attributed to the restlessness resulting from strange conditions. I am inclined to think that if the water and sand provided be of a perfectly suitable character, *Corystes* will remain imbedded throughout the day. (cf. Robertson, l. c. *supra*).

I have noticed, however, that individuals which were inactive and concealed beneath the sand during the day, shewed a marked tendency to activity at night. I have observed on several occasions that my aquarium, containing some half-dozen of these crabs, was the scene of distinct excitement and activity late at night; the crabs had emerged from the sand, and were restlessly hobbling about on the surface, as though in search of food. Although I cannot make a final statement upon the point, all my experiences incline me to the view that *Corystes cassivelaunus* is a nocturnal animal; it conceals itself in the sand by day as a protection from sight-feeding fishes, but emerges at night for food and recreation. If these habits were absolutely constant, we should expect to find the eyes of *Corystes* undergoing retrogressive changes, as, for example, in the case of *Pinnotheres*. Such is not the case, however, for the eyes are capable of forming distinct images, as well as, no doubt, of distinguishing light from darkness.

(b) Respiratory Currents. We have seen that Gosse observed a current of water setting upwards from the buccal region of the crab

through the antennal tube, and carrying upwards the water which had previously bathed the gills. This current was caused, according to Gosse, by the "vigorous vibration of the foot-jaws." The crab observed by Gosse was sitting on the top of the sand—not beneath it.

If some sea-water be coloured by the addition of a little Chinese ink, or finely powdered carmine (the former is the better material), and if a few drops of the coloured water be added to the water in the neighbourhood of the antennal tube of a buried crab, it will invariably be found that the current which sets through the antennal tube is from above downwards, and not *vice versa.* The same current may often, and indeed generally, be shewn to exist, even when the crab is not imbedded in the sand.

It will then be noticed that the coloured water is sucked between the hairs of the antennal tube, and passes downwards and backwards to the prostomial chamber. Here, in front of the labium, the current divides into two streams, one right and one left, which pass outwards and backwards into the right and left branchial chambers respectively. Finally, the coloured stream emerges from the branchial chamber beneath the edge of the branchiostegite, not at any one point, situated either anteriorly or posteriorly, but along its whole extent, and especially between the bases of the legs.

The direction of this current through the branchial chamber is the reverse of that which has hitherto been recognised in all other Decapod Crustacea. In these (*e.g.*, *Maia, Cancer, Carcinus, Astacus*) the current which bathes the gills is known to enter this chamber beneath the branchiostegite, and to emerge in front by the lateral aperture at the side of the mouth. The normal peribranchial current in Decapod Crustacea is from behind forwards; I shall, therefore, term the current of the buried *Corystes* a "reversed current," and shall speak of the whole phenomenon as a "reversal" of the normal current.

Although *Corystes cassivelaunus* constantly exhibits this reversed current when imbedded in the sand, yet it is occasionally possible to observe the normal current in the same specimen when the animal is not buried. The coloured water is then rejected when added near the antennal tube; but if deposited near the bases of the legs, is sucked inwards, and eventually emerges from the branchial cavity into the prostomial chamber, and thence passes either directly to the exterior or forwards by way of the antennal tube. When the normal current is at work it frequently happens that the exopoditic palps of the maxillipeds begin to vibrate. The action of these palps still further intensifies the force of the exhalent currents, and at the same time disperses the streams of water laterally, *i.e.*, the water, instead of passing to the exterior anteriorly in an even stream, is partially diverted to the sides of

the crab's body, and is scattered outwards and laterally by the vigorous lashings of the exopoditic palps.

Gosse's observations on the respiratory currents of *Corystes cassivelaunus* are thus seen to be incomplete rather than inaccurate. A current *may* be directed outwards through the antennal tube, and the effete water from the branchial chamber *may* be carried away by that channel; but such a direction of the current in *Corystes cassivelaunus* is not constant, as Gosse believed, or even usual. Moreover, when the crab is imbedded in sand, the current is always reversed, except for a few seconds now and then, when the crab desires to eject distasteful particles which have entered the prostomial chamber with the respiratory current. Under such circumstances the reversed inhalent current through the antennal tube is temporarily replaced by a forcible exhalent current. But as soon as the desired ejection has been effected, the reversed current is again set up. This voluntary inhibition of the reversed current can be easily demonstrated by the addition of carmine to the water setting through the antennæ. Oddly enough, a weak solution of Chinese ink is less distasteful to *Corystes* than a mixture of powdered carmine and sea-water.

(c) Cause of the Currents. The direction of the respiratory currents is exclusively due to the movements of the scaphognathite, the valve-like and highly muscular appendage of the second maxilla, which is known to produce the regular respiratory currents of other Decapoda. H. Milne-Edwards first demonstrated the important *rôle* played by the scaphognathite in Decapod Crustacea; and he maintained that the direction of the respiratory current was absolutely constant, *i.e.*, from behind forwards in all Decapods (1839, p. 136). De Haan (1850, p. 117) has indeed suggested that the current to the branchiæ passes from before backwards; but his remarks on this subject are obviously the result of mere inference, and are not determined by actual experiment. He states, for example, that in *Portunus* the inhalent current sets inwards not only through the aperture between the base of the cheliped and the edge of the branchiostegite, but also through the anterior aperture at the side of the mouth. Experiments on *Portunus* have shewn me that this is quite devoid of foundation; the water certainly enters—in part—through the former of these apertures, but the aperture at the side of the mouth is invariably exhalent in function.

In the case of *Corystes* I observed the action of the scaphognathite by removing the three maxillipeds and the edge of the pterygostomial fold of a living specimen. The scaphognathite was completely exposed by this preparation, and its movements were readily followed.

When the normal current—from behind forwards—was at work, the propulsion of the water could be seen to be effected by a sharp, prompt

blow dealt by the posterior lobe of the scaphognathite, which was succeeded by an undulatory movement from behind forwards of the remaining part of the scaphognathite. As the crab lay on its back the anterior lobe could finally be seen to descend slowly and gently upon the anterior edge of the roof of the chamber, gliding along, and, as it were, stroking its polished surface.

When the current is reversed, however, the action of the anterior lobe is quite different; it strikes the water in front with a prompt, decisive blow, and this is succeeded by an undulatory movement of the rest of the scaphognathite from before backwards. The water lying between the valve and the roof of the chamber is thus driven backwards into the branchial cavity. The action of the scaphognathite is fairly rapid, but after a little observation, checked by the employment of coloured water to test the currents, it becomes quite easy to detect with certainty the direction of the current by inference from the movements of the scaphognathite alone.

The action of the exopoditic palps of the maxillipeds in causing currents has already been described. Such currents are purely accessory, and Gosse (1865, p. 130) and De Haan (1850, p. 117) have undoubtedly erred in assigning to the maxillipeds an important share in the production of respiratory currents.

V. Evolutional Significance.

The habits of *Corystes cassivelaunus* described above seem to me to demonstrate the adaptive nature of the entire organization of this Crustacean, and slight consideration is all that is required to enable a naturalist to recognise the utility of these adaptive features.

The burrowing habit is useful as a mode of concealment from enemies. The elongation and smoothness of the carapace, and the elongated claws of the four hindmost pair of thoracic legs, are all features usefully correlated with the specialization of the crab for a sand-burrowing existence.

The elongation of the antennæ and the arrangement of the hairs upon them, the double bend of their basal joints, the structure of the parts bounding the prostomial chamber, and the arrangement of hairs upon them, are characters which, in conjunction with the reversal of the respiratory current, adapt the respiratory mechanism of the crab in a remarkably complete manner to an arenicolous mode of life. The antennal tube enables the crab to draw its supplies of water directly from the superincumbent reservoir of water, while the arrangement of hairs is such as to constitute a sieve, keeping the sand away from the respiratory organs.

The upright position of the crab is itself a most unusual feature, and is correlated with the formation of an elongated antennal tube; the posterior position of the legs is functionally correlated with the adoption of the upright attitude.

VI. Analogies.

A reversal of the respiratory current similar to that which I have just described in *Corystes* also takes place under certain conditions in the allied form *Atelecyclus heterodon.* The habits of this crab are much more complex than those of *Corystes*, and will form the subject of a later article.

An elongation of the antennæ, and their conversion into an antennal tube by the interlocking of hairs along their margins, also takes place, as I have recently discovered, in an East Indian Crustacean, *Albunea symnista,* Fabr., which belongs to the Hippinea among the Macrura Anomala (Anomura). In this type, however, the antennal tube is formed by the first and not by the second pair of antennæ. The antennal tube has obviously been produced independently in *Corystes* and *Albunea,* and affords a remarkable example of homoplastic modification. In all probability the function of the tube is the same in both cases, but no direct observations on this head in the case of *Albunea* have yet been made.

It seems to me not unlikely that further observation of the habits of *Hippa talpoida* of the American coasts will reveal an essentially similar sieve-like function for the curiously bent and setose second antennæ of that animal.

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Contributions to Marine Bionomics.

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II. The Function of Antero-lateral Denticulations of the Carapace in Sand-burrowing Crabs.

THE antero-lateral margins of the carapace in many of the crabs of our own and of foreign coasts are beset with a row of teeth or spines, which vary in character and number in different species and genera. In the Oxyrhyncha (Spider-crabs) the whole surface of the carapace is generally studded with spines and stiff hairs of a peculiar character, but there is no general restriction of these processes of the carapace to the antero-lateral margins of the body. These crabs, moreover, do not adopt burrowing habits. Their armature of spines, tubercles, and hairs is employed, as is well known, for protective purposes: in some cases possibly as an actual defence against attack, in others (*i.e.*, *Eurynome aspera*) as a means of protective resemblance to their surroundings; but in the great majority as mere pegs and hooks for the fixation of foreign bodies, such as algæ, hydroids, polyzoa, and ascidians, for purposes of concealment and disguise.

In the Catometopa (Land-crabs, etc.) the carapace is usually smooth over its whole surface. These animals often burrow in sand, but for the most part their burrows are permanent subterranean tunnels and chambers.

In the Cyclometopa, however—the group which includes most of our commoner British crabs—the back of the carapace is generally smooth, while the antero-lateral margins are in most forms conspicuously serrated. Most of these animals inhabit sandy or gravelly areas, and show a marked propensity towards burrowing habits. Their burrows are never* permanent channels or tunnels in the sand, but are mere temporary excavations, the sand, mud, or gravel being in actual contact with their bodies when imbedded.

So far as I am aware no one has hitherto elucidated the remarkable constancy of antero-lateral serrations of the carapace in this group of crabs. I here present evidence which tends to show that the presence

* *Scylla serrata* of the Natal coast *appears* to be exceptional in this respect. (KRAUSS, *Die Südafricanischen Crustaceen,* 1843, p. 12.)

of conspicuous serrations on these margins of the carapace is functionally related to the exigencies of respiration when these animals are buried in sand.

The marginal teeth are perhaps best developed and most conspicuous in crabs of the family Portunidæ (Swimming-crabs). As M. Alphonse Milne-Edwards has remarked: "Je ne connais aucun Portunien où le bord latéro-antérieur de la carapace soit entier ou armé d'épines arrondies ou de tubercules obtus." (1860, p. 202.)

In *Bathynectes longipes* there are five sharp-pointed teeth on each of the antero-lateral borders. These teeth increase in size regularly from before backwards, and the posterior tooth is a particularly stout and sharp structure. This crab is almost invariably an inhabitant of sandy areas (*e.g.*, Mounts Bay in Cornwall); and the individual whose habits I am about to describe was also dredged upon a bottom of fine sand in the neighbourhood of the Eddystone.

In an aquarium containing sand the crab burrows into the sand just beneath the surface, leaving its eyes and the transverse slit-like aperture of the buccal frame exposed. The crab is actually imbedded up to the anterior edge of the external maxillipeds; but it pushes away the sand in front of it by means of these appendages, and when at rest maintains these appendages in a sloping posture, so that they act as a quadrangular sieve-like fence in front of the buccal area. This happens both in very fine siliceous sand and in fine shell sand. The crab was not seen at any time to go completely beneath the surface, though I do not mean to imply by this that the crab never buries itself entirely. This may or may not be the case. *Atelecyclus heterodon* is another sand-burrowing crab, whose habits I have studied for a much longer period; and this crab has very diversified habits. It may remain partially imbedded at the surface of the sand, with its eyes and a broad funnel formed by the second antennæ alone protruding, or it may disappear completely beneath the sand to a depth of several inches.

When the crab (*Bathynectes longipes*) is partially imbedded in the sand as above described, it may be noticed that the chelipeds are flexed and approximated to the under side of the antero-lateral regions of the carapace in an attitude precisely similar to that assumed by *Atelecyclus heterodon*, or the Oxystome crab *Matuta*, under the same conditions (1897). The position of the cheliped is such that the marginal teeth of the antero-lateral region of the carapace exactly overhang the slit-like orifice between the distal half of the cheliped (carpopodite and propodite) and the pterygostomial fold of the carapace. There is thus produced on each side of the crab, between cheliped and carapace, a channel similar to that which would be produced by the approximation in parallel planes of two flat plates. This channel communicates below with the

afferent (inhalant) aperture of the branchial chamber, which is situated at the base of the cheliped, and opens above through the notches between the teeth of the antero-lateral margins of the carapace. Since the back of the crab is covered with sand, it will readily be understood from this description that the antero-lateral teeth act as a coarse sieve or grating placed over the orifice of this accessory channel, and that they prevent the accidental intrusion of sand-particles into the lumen of the channel, a function which it was easy to determine that they efficiently discharged.

The pair of accessory channels produced by the approximation of chelipeds to carapace I propose to term the "exostegal channels," owing to their situation on the external face of the branchiostegite. I show elsewhere (1897) that these channels probably represent in a generalised condition certain remarkable accessory afferent branchial canals of the Oxystome Brachyura, which attain their most specialised form and relations in *Ebalia* and other Leucosiidæ.

M. Alphonse Milne-Edwards (1860, p. 207) states that in the Portunidæ "les mains ne sont jamais conformées de facon à pouvoir s'appliquer exactement contre la région buccale, ainsi que cela se voit chez quelques autres Brachyures nageurs tels que les Calappes et les Matutes." This contrast is quite in accordance with my view, that the afferent channel of the Portunidæ represents a primitive and relatively unspecialised type, from which the highly elaborate canals of the Oxystomata have been derived.

That these accessory channels in the Portunidæ are functionally connected with the respiratory process, was demonstrated by me in the case of *Bathynectes longipes* in the following manner:—

When the crab was partially imbedded in sand with its face close to the front of a square glass aquarium, in the attitude already described, it could be seen that beneath the body of the crab was a shallow ventral water-chamber, free from sand. The crab was resting with its body in an approximately horizontal plane. Sand-particles were supported over the orifice of the exostegal channel by the sieve-like row of teeth along the antero-lateral margins. Some water, coloured black with Indian ink, was then added by means of a pipette to the water lying above the slit between cheliped and carapace. The coloured water was at once sucked downwards between the grains of sand into the exostegal channel in waves which apparently corresponded to blows of the scaphognathite, and after a few seconds emerged in a black stream out of the afferent orifice of the branchial chamber situated in front of the mouth. It was quite clear that the water passed downwards through the exostegal channel to the afferent aperture at the base of the cheliped, and that it entered the branchial chamber by this aperture.

Similar observations and experiments were made upon numerous specimens of *Atelecyclus heterodon*, a crab belonging to an altogether different family. In this crab the antero-lateral margins are provided with as many as nine teeth, but the function of the teeth was found to be essentially similar. Owing to the different form of the body, and the different shape of the cheliped in the two crabs, the orifice of the channel between cheliped and carapace is of greater relative extent in *Atelecyclus* than in *Bathynectes;* but the length of the denticulated margin of the carapace was found to correspond precisely with the extent of the inhalant gap in each case. The following conclusions may be drawn, therefore, from these observations:—

(1) Antero-lateral denticulations of the carapace in crabs may subserve a sieve-like function.

(2) The extent of the denticulated area corresponds with the extent of the inhalant gap between the carapace and the cheliped when the latter appendage is approximated to it in the flexed position.

It is also obvious that a new function must be ascribed to the chelipeds of sand-burrowing crabs provided with antero-lateral denticulations of the carapace. In such cases the chelipeds act as organs temporarily subservient to the respiratory process by providing a broad operculum to the exostegal channel. Attention may be recalled in this connection to the fact elucidated by Milne-Edwards in 1839, that in the Leucosiidæ the floor of the afferent branchial channel is also provided by one of the appendages, in this case by the external maxillipeds. The relations of the afferent channel in the Leucosiidæ to the external channel which I have now described in the Cyclometopa are discussed by me in the paper to which reference has already been made (1897).

The subservience of the chelipeds to the respiratory process enables me, moreover, to explain the function of a remarkable spine which in the Portunidæ is almost universally present on the inner margin of the distal extremity of the carpal joint (carpopodite or wrist) of the cheliped. This carpal spine, though usually strong and conspicuous, presents various minor modifications of form which are employed by systematists in the discrimination of different species.

The appearance of the spine in *Bathynectes longipes* is represented by Bell and Risso. When the cheliped is fully extended the carpal spine projects freely from its anterior margin; but when the propodite is flexed towards the proximal part of the cheliped, it is arrested at a certain angle with the carpopodite by the carpal spine in question. If now the arm (meropodite) of the cheliped be approximated to the carapace in the position requisite for the completion of the exostegal canal, it

will be found that the angle at which the propodite has been arrested by the carpal spine is precisely the angle required for the proper apposition of cheliped to carapace in connection with the respiratory process. The carpal spine acts then as a stay or barrier to excessive flexion of the cheliped. Its function corresponds, therefore, in part to the function of such skeletal processes as the olecranon of the human ulna, which prevents excessive extension of the arm. Examination of a series of Portunids reveals that the variations in the form of the carpal spine in different species and genera are all functionally correlated with the different shapes and proportions of the carapace, and of the segments of the cheliped in the forms examined; the result in all cases being that the shape of the carpal spine is adapted to ensure the due amount of flexion of the cheliped for the completion of the respiratory channel between cheliped and carapace.

A similar function seems also to be discharged by the enlarged posterior spine of the antero-lateral margins in *Bathynectes longipes*, since the carpopodite presses upwards against it during flexion of the cheliped. An examination of preserved specimens of the Mediterranean *Lupa hastata*, and of the American *Callinectes sapidus*, in which the posterior spine is greatly elongated, seems to me to support this view, though I do not regard the evidence in this case as altogether unequivocal. A complete explanation of the enlargement of this posterior antero-lateral spine should also throw light on the great epibranchial spines of the Oxystome genus *Matuta*, and of the Lencosiid genera *Iphis* and *Ixa*. In the latter cases any relation between the development of the spines and the formation of an inhalant chamber between cheliped and carapace is precluded by the known course of the afferent current in a gutter running between the pterygostomial plate and the exopodite of the third maxilliped.

The phenomena presented by the respiratory processes of these sand-burrowing crabs throw light, as it seems to me, not only on the problem of the utility of a number of morphologically trivial, but systematically important features of Decapod Crustacea, but also on an altogether different problem, viz., the phylogeny of the Brachyura Oxystomata. Crabs of the latter group are all characterised by their sand-burrowing habits of life. Similarity of habits often induces homoplastic changes of form in types genetically distinct; but there are certain significant details of structure in the different Oxystome types which appear to me to be only explicable on the view that these crabs are descended from ancestors in which the form of the body closely resembled that of sand-burrowing Cyclometopa in being provided with antero-lateral serrated margins, and in which the chelipeds were employed for the production of an extensive inhalant channel, completely roofed over by the projecting teeth of the carapace. For a fuller discussion of this subject I must refer the reader to another paper to be published in the *Quarterly Journal of Microscopical Science* (1897).

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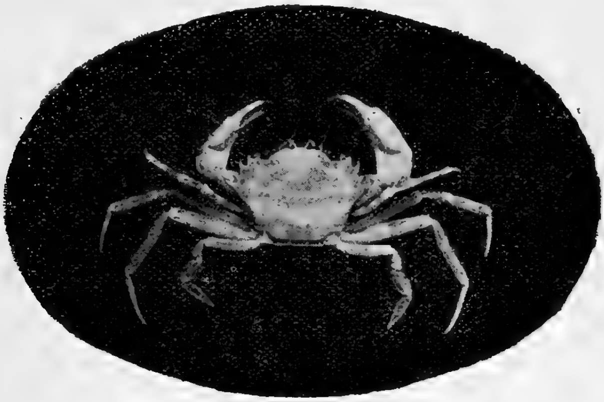

FIG. 1.

Fig. 1.—*Bathynectes longipes.* Dorsal view, showing the five teeth of the antero-lateral margins. The chelipeds are in a half-extended condition; their propodites (hands) are shown resting against the carpal spines. The specimen shows an abnormality in the union of the two anterior marginal teeth of the right side to form a single bifid tooth.

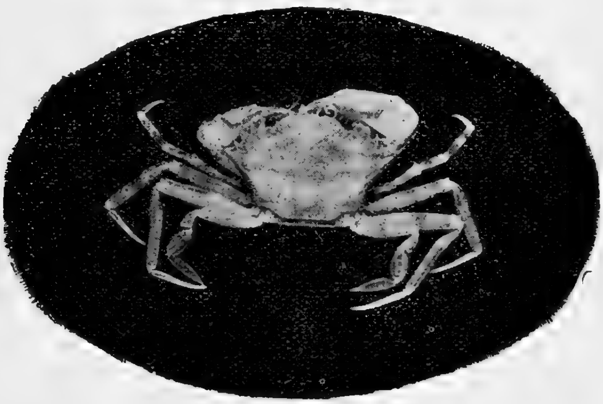

FIG. 2.

Fig. 2.—*Bathynectes longipes.* Dorsal view, showing the position of the chelipeds after flexion of the wrists (carpopodites) as well as of the hands. The left cheliped is in the attitude assumed by the crab when imbedded in sand; the antero-lateral teeth are seen to form a sieve above the orifice of the inhalant gap between cheliped and carapace. On the right side the arm (meropodite) of the cheliped does not rest in its proper position beneath the enlarged posterior marginal tooth; hence the inhalant gap is imperfectly formed, and its aperture is imperfectly covered by the marginal teeth.

III. The Systematic Features, Habits, and Respiratory Phenomena of Portumnus nasutus (Latreille).

The crab whose habits I now describe has not previously been recorded as an inhabitant of British seas. I found two specimens, both male, imbedded in a patch of coarse shell sand on the south side of Drake's Island at low water, spring tides: one on August 11th, 1896, and the other on the following day.

1. Nomenclature.

My first impression on noticing this remarkable little crab was that I had an abnormal specimen of a young *Carcinus maenas* before me; but the possibility of such a leap from the normal as the frontal area of this specimen would produce on a variation-chart was soon disposed of by Professor Weldon, and we identified the crab with the *Portunus biguttatus* of Risso (1816), now usually known under the name *Platyonichus nasutus* of Latreille (1825, p. 151; cf. also Milne-Edwards, 1834; Costa, 1853, p. 11; Carus, 1885).

The genus *Platyonichus* of Latreille (1818) was originally coextensive with the genus *Portumnus* of Leach (1815), Latreille having simply altered Leach's name owing to its similarity to the name *Portunus*, with which he feared it might be confused. Dana (1852), however, and Bell (1853), showed that the species included within the genus *Platyonichus* were separable into two well-marked groups, which were accordingly named by these writers *Platyonichus* and *Portumnus* respectively, the latter name being reapplied to the group which included Leach's type, viz., *Portumnus latipes*. It is to the latter group that *Platyonichus nasutus* belongs, so that I must refer to it for the future as *Portumnus nasutus*.

It is true that the earliest specific name applied to the present species is *biguttatus* of Risso (1816), the name *nasutus* of Latreille (1825) being nearly ten years later. Since, however, the species has been invariably referred to under Latreille's name, probably owing to the influence of Milne-Edwards' adoption of it, I submit that we have here an exceptional case which demands exceptional treatment. The rule of priority provides a decisive method of dealing with a confused and complicated synonymy; but its application in the present case could not be urged on such grounds, and would be distinctly inconvenient. I shall therefore adhere to the employment of Latreille's name *nasutus* in referring to the species under discussion. In the event, however, of possible differences being discovered between Mediterranean and Atlantic races of this species, I would point out that Risso's name

was created for Mediterranean specimens, while Latreille's type came from the west coast of France.

2. Generic Characters.

The genus *Portumnus* takes its place together with *Carcinus, Platyonichus,* and *Polybius* in the Platyonichinæ, a sub-family of the Portunidæ distinguished from the Portuninæ by the absence of lateral ridges on the prælabial plate, and by the absence of a distinct accessory lobe to the endopodite of the first maxillipeds.

Portumnus is distinguished from *Platyonichus* by having the dactylus of the fifth thoracic leg of a slender lanceolate form, and the carapace not broader than long. In *Platyonichus* the dactylus is elliptical or broadly oval, and the carapace is broader than long. To these distinctions I may add that in *Platyonichus* the interorbital margin is at most tridentate or quadridentate, while in *Portumnus* the inner angle of the orbit contributes a distinct accessory tooth to the frontal margin, rendering this margin five-toothed, as in *Polybius Henslowii.*

3. Specific Characters.

The two species of the genus which alone are known to me are *P. latipes* (Pennant) and *P. nasutus.* A description of the former species may be found in Bell (1853) under the name *Portumnus variegatus.* The characteristic features of *P. nasutus* are as follows:—

Frontal area projecting in front of the orbits in the form of a conspicuous triangular lobe with gently undulate lateral margins.

The undulations mark the subdivision of the interorbital margin into five rounded lobules, which correspond to the five interorbital teeth of *P. latipes.* The interorbital lobe bends downwards in front.

The carapace is relatively broader than in *P. latipes,* so that the antero-lateral margins make a sharper angle with the median transverse axis.

The orbit shows two superior fissures and one inferior fissure (*pace* Latreille and H. Milne-Edwards, who mention only one superior fissure), while in *P. latipes* the orbit is stated to be either entire (Bell; Leach, 1815) or provided with a single fissure above (H. Milne-Edwards, 1834).

The basal joint of the second antenna is movable.

4. Colour.

The colour of the carapace of *Portumnus nasutus* is thus described by Risso (1816, p. 31)—"yellowish-white, adorned with two great spots of coral-red . . . The red spots are larger in the female than in the

male." On account of the presence of these spots Risso named the species *Portunus biguttatus, portune à deux taches, portune bimaculé* (p. 25).

Costa, on the other hand (*Addizioni*, 1853, p. 11), describes the colour as "livid olive-brown tending towards purple; that of the feet and of the inferior face more pallid. In fresh specimens one may sometimes observe two rose-coloured spots in the middle of the carapace, which vanish after death."

Of my own specimens the larger one was of a uniform dull greenish yellow colour, the smaller one having the carapace and basal joints of the legs absolutely white, and the two terminal joints of the four posterior pairs of thoracic legs coloured pale brown and amethyst-violet. No reddish spots were visible in the living specimens. It is possible that these spots are only to be observed in the breeding season, and that they are due to the colour of the reproductive glands showing through the carapace. Such a phenomenon is at any rate described by Risso for *Bathynectes longipes*. He states (1816, pp. 30, 31): "La femelle, dans le temps des amours, est ornée de deux grandes taches d'un rouge foncé sur la partie antérieure du têt." The eggs of the latter species are described as "d'un rouge aurore," which would sufficiently account for the red colour of the ovarian regions before deposition of the ova; those of *P. nasutus* are described as "d'un jaune doré." Risso states that the eggs of *P. nasutus* are laid in May and August.

5. Sand-burrowing Habits.

The habits of *Portumnus nasutus* have hitherto been very imperfectly described. Risso (1816, pp. 25–31) states simply that at Nice the crab inhabits "la région des polypiers corticiféres" (p. 25), or "la région des coraux" (p. 31). Latreille's specimen (1825, p. 151) was obtained by D'Orbigny on the coast of La Vendée, which probably implies a sandy habitat, especially as Latreille's specimens of "*Platyonichus variegatus*" (*Portumnus latipes*) were obtained by the same naturalist on the same coast (*Nouv. Dict. d'Hist. Nat.*, 1818), and the latter species is known to have sand-burrowing habits.

My own observations are, however, unequivocal. The specimens were found burrowing in coarse shelly gravel, and when the crabs were introduced into an aquarium containing a deep layer of the same gravel they were observed to burrow into it at once with extreme agility until their bodies were completely covered to a depth of an inch or more. The act of burrowing is effected by means of the hinder thoracic legs, as is usual among Portunids. The crabs can also burrow in fine siliceous sand.

When imbedded, *P. nasutus* seems always to adopt a nearly horizontal

position—not the upright attitude exhibited by *Corystes cassivelaunus* (this Journal, 1896, p. 223). The anterior part of the body is, however, generally a little higher than the posterior.

6. Respiratory Currents.

Under these circumstances, *Portumnus nasutus* exhibits a reversed water-current through its branchial chamber, though this is much more difficult to demonstrate in the present species than in the case of *Corystes*. The method I adopted was as follows:—

The depth of gravel in the aquarium was so regulated that the crab could not burrow far beneath the surface. The fragments of sand and shell which lay upon the front of its carapace and upon its inter-orbital lobe were then gently removed, one by one, with a pair of fine forceps, until the aperture of the buccal frame was exposed. These proceedings were, however, incessantly watched by the crab, which, not unnaturally, did not hesitate to disturb my preparations whenever it conceived that there was due cause for alarm. I therefore took the precaution to leave some fragments of shell over its eyes, and thus did not seriously disturb its impression that it was safely ensconced. I eventually succeeded in getting the crab so suitably situated that, on the addition of a little black-coloured water by means of a pipette to the region in front of the crab's maxillipeds, I had the satisfaction of seeing the water sucked inwards on both sides, to reappear again in a pair of streams at the base of the chelipeds. The two exhalant streams rose above the surface of the sand in a pair of clouds, one on each side of the body. Suddenly, and without warning, the normal current was set up, and then the lateral clouds of inky water were rapidly sucked in again on each side, to re-emerge again a second or two afterwards in a continuous stream in front of the mouth. Without this kindly co-operation on the part of the crab it would have been difficult, if not impossible, to get so successful a demonstration of the reversal of the currents. One of the most interesting phenomena presented by this crab is indeed the frequency with which, when under observation, it will alternate the direction of the respiratory currents.* It may even suspend the respiratory currents altogether for long intervals; *e.g.*, for as long as fifty-five seconds. At such times there is absolutely no movement in the surrounding water.

7. Utility of Specific Characters.

The interorbital prolongation of the frontal area, which gives both its name and most peculiar feature to the species *Portumnus nasutus*, is

* Probably to eject distasteful particles. This is undoubtedly the explanation of similar phenomena in the case of *Corystes*. (See this Journal, vol. iv. 1896, p. 230.)

a feature usefully correlated with a habit of burrowing in coarse shelly gravel. It acts as an efficient buckler for the protection of the anterior sense-organs; but its unusual size and its downward bend seem to be more directly correlated with the reversal of the branchial currents, which I have shown to take place when the crab is imbedded. The advantage of reversal in the present case is a point to which I shall recur when dealing with the phenomenon in a more general manner; but, granted the reversal, the utility of the possession of a stout triangular shelf over the inhalant orifices is obvious after a study of the animal's habits and of the nature of the objects amid which the crab excavates its dwelling-place. In *Corystes,* which lives in fine sand, the inhalant antennal tube has been shown (1896) to subserve the double purpose of a supply pipe and a sieve. In *P. nasutus* a sieve is unnecessary so long as the crab inhabits coarse shell-gravel, the fragments of which are too large to enter the respiratory channels; and this appears to be the specific habit of the crab. But if the anterior inhalant apertures (during reversal) were altogether unprotected, the pointed fragments of shell might easily penetrate the inhalant orifices (during reversal), and so occlude their lumen. Such occlusion would prevent the crab from burrowing in the kind of material most suitable to its respiratory organisation, and thus expose the animal to increased risks of destruction by its ever-watchful enemies among fishes. The overhanging buckler provided by the prominent frontal lobe acts, however, as a very efficient means of supporting the shell-fragments well above the inhalant orifices—a function the existence of which I do not throw out as an academical suggestion, but the value of which I had frequent opportunities of observing and appreciating in my aquaria.

The interorbital lobe of *P. nasutus* is remarkably similar to the frontal protuberance of *Carcinus maenas* in the *Megalops* stage, which becomes reduced in later stages of development. Since I have found no indications of a reversal of the respiratory currents in the latter species, I am inclined to believe that the retention of this larval feature in *P. nasutus* is to be correlated with the reversal of the currents which occurs, as I have shown above, in this type; while its eventual loss in *Carcinus maenas* is to be indirectly attributed to the lack of any further use for it after the larval stages. The larval forms of *P. nasutus* are at present, however, unknown, and it is impossible to support this view with the necessary embryological facts.

The other specific characters of *P. nasutus* (viz., breadth of carapace, retention of two supra-orbital fissures, mobility of basal joint of second antenna) are not new features acquired within the history of the present species, but are merely heirlooms from Portunid ancestors of less specialised habits. It is not their presence in *P. nasutus* which is to

be accounted for, but their absence in *Portumnus latipes.* The elucidation of those features will be attempted in a subsequent article dealing with the habits of the latter species.

In conclusion I may add that a good figure of *P. nasutus* is given in Costa's classical memoir on the fauna of the Bay of Naples (1853).

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THE MORPHOLOGY OF THE MOLLUSCA.

THE recent publication of a number of new manuals and monographs dealing with the Mollusca offers a favourable opportunity for a review of our knowledge of this great phylum of the animal kingdom. It is not fifteen years since Professor Lankester's classical article on Mollusca was published in the *Encyclopædia Britannica*, yet the contributions to Molluscan morphology since that date have been not only numerous, but in many cases of prime importance.

The older method of inquiry, that of the comparison of types more or less arbitrarily selected from different groups, has been succeeded by investigations more directly influenced by the idea of evolution. The comparison of types has been replaced by the study of groups. The foundations of the morphological edifice were laid upon the former method; the superstructure and details are the result of the latter. Homologies having been to a large extent determined, we now seek phylogenies. It happens also from time to time that the detailed study of a group with the object of reconstructing the phylogeny of its members leads occasionally to the discovery that homologies based on the simple method of anatomical comparison turn out to be nothing more than analogies—recurrent examples of similar modifications.

One result of these phylogenetic inquiries has been the concentration of particular attention upon forms which are presumably the most primitive in each group; and great advances have thus been made in our knowledge. Kowalewsky and Marion, Pruvot, Wirén, and Thiele have enormously extended our acquaintance with the Aplacophorous Isopleura; primitive Prosobranchs (Docoglossa and Rhipidoglossa) have been thoroughly investigated by

Haller and Boutan; Bouvier has thrown new light upon the Opisthobranchia by his researches on *Actæon;* Boas and Pelseneer have revolutionised our ideas of the Pteropoda by their work upon *Limacina* among the Thecosomata, and upon *Dexiobranchæa* and other types among the Gymnosomata; the morphology of the Pelecypoda has been further elucidated by Pelseneer's observations upon *Nucula* and other primitive forms, and important contributions to our knowledge of the Cephalopoda were made during the past year by Huxley and Pelseneer in the case of *Spirula*, that last survivor of the ancient types of Decapod Dibranchiates. We doubt if any equivalent group of the animal kingdom, except perhaps the Echinoderma, has been the subject of such productive researches as the Mollusca during the period under consideration; and certainly the phylogenetic method of inquiry has attained no greater triumphs than in the hands of Bouvier, Haller, Pelseneer, and other investigators of the Gastropod and Lamellibranch series.

In the present article I propose to deal more especially with recent contributions to our knowledge of the Molluscan nervous system, reserving a fuller consideration of other questions for a later article.

There is one writer, however, whose views must first of all be dealt with, as on a great number of fundamental points they are opposed to all current conceptions of Molluscan morphology. These views merit some detailed consideration, moreover, for they are based on propositions which are not without a certain appearance of plausibility, and may well serve as test-questions by which to examine into the accuracy of the homologies which have been generally admitted to exist between the different sections of the Molluscan phylum.

Thiele has published his views in a series of lengthy papers, the references to which will be found in the bibliography (23, 24, 25). He regards the Mollusca and Annelida as direct descendants of Polyclad Turbellarians, and

his identifications of homologous organs in the different Molluscan groups are determined, not by a direct comparison of the organisation of these types one with another, but by independent comparisons of the organisation of the different Molluscan types with that of sucker-bearing Polyclads. The group Mollusca is thus made to lose its compactness, and characteristic organs, such as mantle and ctenidium, which have been regarded as homologous throughout the Molluscan series, are interpreted in different ways in the different types, as the exigencies of Thiele's theory demand. One of the first propositions assumed by this writer is that the foot of the Mollusca is simply a colossal enlargement of the ventral sucker of the Polyclad; the suctorial function of the foot in *Chiton* and the lower Gastropoda is pointed to in support of this comparison. A series of more revolutionary propositions is then promulgated in consequence of the necessity under which the author is placed of discovering the primitive body-edge of the Mollusca comparable to the edge of the body of the Turbellaria. This primitive body-edge Thiele identifies by means of the lateral sense-organs which characterise the epipodium in the Rhipidoglossa and the margin of the mantle in Pelecypoda. The epipodium in Gastropoda and the mantle edge in Pelecypoda are thus taken by this writer to represent the sides or edge of the body in the Turbellarian ancestor. The epipodium in Gastropoda and the mantle edge in Pelecypoda consequently separate the dorsal from the ventral regions of the body in those groups. It follows from this that the ctenidia of Gastropoda, which are supra-epipodial in position, are not homologous with the ctenidia of Pelecypoda, which are infra-pallial. How we are to regard the anus, which is dorsal in the one group and ventral in the other, is not explained. But since in operculate Rhipidoglossa the operculum, like the shell, is situated above the epipodium, we are told that the operculum must also be regarded as dorsal in position, as well

as serially homologous with the shell proper. This, in Thiele's eyes, compares well with the condition of affairs in *Chiton*, whose shelly plates are without doubt serially homologous. Moreover, although the existence of an epipodium in *Chiton* has not been hitherto recognised, Thiele argues that, since the pallial fold in this form represents the primitive body-edge, it must also, together with the series of ctenidia which are attached to its lower surface, be regarded as the homologue of the epipodium of the Rhipidoglossa. The ctenidia of *Chiton* are, in fact, regarded as modified epipodial cirri. The consequence of this view is that while the mantle of *Chiton* and the mantle of Pelecypoda are regarded as homologous, the mantle of the Gastropoda is supposed to represent only a portion of the mantle in these other forms, and its projecting rim, similar as it appears to be in the two cases, is held to be a new and secondary formation unrepresented in the Amphineura and Pelecypoda.

Nowhere, however, do we find in Thiele's voluminous writings any explanation of the anomaly which ought to have occurred to him, that while in *Chiton* the anus is "ventral," and lies well beneath the "epipodium" and the last shell-plate, in operculate Gastropods the intestine opens not only above the epipodium, but between the operculum and the shell of the embryo—a relation which could only be represented in *Chiton*, if Thiele's theories were correct, by the situation of the anus between two of the shell-plates upon the back of that animal!

The nervous system of the Mollusca is treated by Thiele with a ruthlessness no less than that which is meted out to the external organs of the body. Let us take the Amphineura first. In this group, if the relations of the nervous system in *Chiton* be taken as typical, we have dorsal to the gut a great ganglionic nerve-ring whose lateral components are usually referred to as the lateral or pleuro-visceral cords. Connected anteriorly with the cerebral

enlargements of this nerve-ring is a pair of ventral or pedal cords, connected with one another by a series of commissures lying beneath the gut, and also with the lateral cords by means of lateral connectives. The lateral cords innervate the pallial sense-organs, gills, and viscera; the ventral cords the musculature of the foot. The lateral cords are regarded by Thiele as the homologues of the lateral cords or nerve-ring of the Turbellarians, and the ventral cords are taken to correspond to the ventral longitudinal nerves of the same forms. So far we find nothing either erratic or original, for the same view has already been taken by Lang (16).

But the novelties begin with Thiele's interpretations of the nervous system of Gastropoda and Pelecypoda. We have already pointed out Thiele's view that the epipodium of Gastropods represents the primitive body-edge. Now at the base of the epipodium in *Fissurella* and *Haliotis* there lies a ganglionic plexus; and this plexus, which takes the form of an incomplete ring, is regarded as the homologue of the lateral cords of Turbellarians and Amphineura. The series of epipodial nerves which connect the epipodial plexus with the upper half of the pedal cords in Rhipidoglossa is compared with the series of connectives between the lateral and ventral cords in Amphineura.

This seems very plausible until one recollects (1) that, the epipodium being infra-rectal, the epipodial plexus is also infra-rectal and thus difficult to compare with the lateral cords of Amphineura, whose "commissure" is supra-rectal; and (2) that, whereas in Amphineura the lateral cords innervate practically the whole of the pallium and viscera, in Rhipidoglossa the epipodial plexus has nothing to do with any other organs except the sense-organs of the epipodium. If the pallium of the Gastropoda is really, as Thiele maintains, a secondary differentiation of the primary pallium of the Amphineura, one would expect that its innervation would also be effected by progressive differen-

tiation of the nerve-centres which supplied the primary pallium, *viz.*, from the lateral or epipodial centres. So far from this being the case, however, Thiele himself (xxv., pp. 587-9) adopts the view that the pallial nerves as well as the pleural ganglia of Gastropoda are secondary derivatives of the ventral or pedal cords.

The recklessness of Thiele's comparisons reaches its high-water mark, perhaps, in his remarks on the nervous system of Pelecypoda. Correlated with the existence of numerous sense-organs (eyes, tentacles, etc.) along the mantle edge, there exists in many forms (*Arca*, *Pecten*, *Pinna*, etc.) a nervous ring around the mantle which may take the form either of a complete ring of peripheral ganglia united by a plexus, or of a circumpallial ganglionated nerve, as was recognised by Duvernoy (5) more than thirty years ago. Since the mantle-lappets of the two sides of the body unite posteriorly above the anus, this pallial nerve-ring lies above the gut. The ring is connected with the cerebro-pleural ganglia by means of the anterior pallial nerves, and with the visceral (parieto-splanchnic) by means of branches from the great posterior pallial nerves. Accordingly Thiele homologises the circumpallial nerve-ring with the lateral cords of *Chiton* and with the epipodial plexus of the Rhipidoglossa.

The first of these homologies seems not unreasonable, for no one disputes the homology between the mantle of *Chiton* and that of Pelecypoda. Moreover Kowalevsky's discovery that *Chiton* in its later embryonic phases is provided with a pair of transitory eyes which lie outside the velar area and have some close connection with the lateral nerve-cords, renders this comparison particularly worthy of attention. But how the circumpallial nerve of Pelecypoda can be in any sense homologous with the epipodial plexus of Gastropoda, when the latter structure lies beneath the gut and has no connection with the cerebral ganglia, either directly or by the intermediation of the pleural ganglia, it

is altogether impossible to conceive. And this is not all. The posterior connection between the circumpallial nerve of Pelecypoda and the visceral ganglia is compared by Thiele with the posterior connectives between the lateral and ventral cords of Amphineura; and the time-honoured visceral nerve-cords of Pelecypoda, with the visceral (parieto-splanchnic) ganglia upon them, are homologised with the ventral cords of the Amphineura. To reveal the absurdity of these comparisons it is sufficient, I think, to remind my readers that the ventral cords of *Chiton* are concerned exclusively with the innervation of the musculature of the foot; while the visceral cords of Pelecypoda innervate the body-wall, ctenidia and viscera, in addition to the posterior adductor muscle. How these supposed homologues of the ventral cords of *Chiton* have come to assume so many of the functions of the lateral or pallio-visceral cords, is not explained; and since Pelecypoda possess a pair of pedal ganglia in the foot, as typical in their relations as those of any Gastropod—in *Nucula* to the extent even of having separate cerebro-pedal and pleuro-pedal connectives (18, 19)—it seems profitless to pursue these ill-balanced speculations any further.

The utmost ingenuity cannot overcome the fact that there is a fundamental disparity between the Turbellarian and Molluscan body. This disparity is revealed by embryology; but to embryology Thiele pays scant attention. Thiele's argument is practically this (24, p. 504),—that the only route from Cœlenterates to Bilateralia is *viâ* the Ctenophores to Polyclads, and that Annelids and Molluscs are consequently to be derived from Polyclad ancestors. Embryology seems to me, however, to point to two lines of descent at least, from the Cœlenterates to the Bilateralia. In each case the oral surface of the Cœlenterate ancestor became the ventral surface of the Bilateral descendant; but along one line of descent the primitive mouth or blastopore retained its ancestral form as a simple circular orifice in the

middle of the ventral surface, and opened into a gastral cavity devoid of an anal orifice (Polyclads); while along the line of descent which led to the Annelida and Mollusca the blastopore elongated along the ventral surface, as Sedgwick has so ably contended, its lips coalesced except at the two extremities, and these open ends constituted the mouth and anus of the Cœlomate descendants. Thiele has altogether overlooked the significant behaviour of the blastopore in Annelidan and Molluscan embryos; and since no similar modification of the blastopore is known in the case of Turbellarians and Trematodes, in which groups the absence of an anus is so marked a characteristic, we are amply warranted, I think, in drawing the conclusions which I have emphasised above.

The admission of this distinction is however fatal to any theory of the Polyclad ancestry of the Mollusca. The foot of the Mollusca is a development of the fused lips of the elongated blastopore, and can in no case be homologised with the ventral sucker of Turbellarians which lies entirely behind the blastopore. The same remark applies to Lang's comparison of the Molluscan foot with the ventral surface of the Turbellarian. The foot is undoubtedly part of the ventral surface of the Mollusc, and as such may be compared, in a general way, with the creeping surface of a Planarian; but as a specialised organ, developed from the fused lateral margins of a slit-like blastopore, it has no homologue in the organisation of the Turbellaria.

Let us now see what light has been thrown on the problems of Molluscan morphology by the researches of other investigators.

The visceral commissure.—One of the greatest difficulties in comparing the Amphineura with the Gastropoda or other Molluscan types has long been the fact that the lateral or pleuro-visceral cords of *Chiton*, which innervate the gills, viscera, and mantle, are united to one another posteriorly by a "commissure" lying above the rectum;

whereas the visceral commissure of Gastropoda and Pelecypoda, etc., lies below the intestine.

A little care in the use of words would have prevented much of the confusion and controversy which has arisen on this subject of the position of the visceral commissure. Words, as Bacon phrases it, put constraint upon the intellect, and there is no doubt that the disagreement and perplexity of naturalists concerning this point have been caused by one of the *idola fori* which they have themselves set up, rather than by any intrinsic incompatibility in the facts themselves. If the language must still be maintained, I must at least point out that there are commissures and commissures, and that one may be a commissure in fact, and another only in name. The suprarectal "commissure" in Amphineura is ganglionic, and, like the rest of the pleuro-visceral nerve-ring, is formed *in situ* by delamination from the ectoderm (15). It is not a commissure in the strict sense of the word, but an integral portion of an annular central nervous system. But the visceral loop of other Molluscs consists merely of nerve-fibres connecting usually a couple of visceral ganglia with one another, and with the pleural ganglia. Now nerve-fibres are outgrowths from nerve-cells, and if two groups of nerve-cells should happen to take a somewhat deep-seated position in the body before their fibres have grown out (which is not a rare embryological phenomenon), there should be nothing incomprehensible in their fibres taking the shortest route and meeting beneath the gut instead of over it. Clearly, therefore, the ventral position of the visceral commissure in most Mollusca by no means precludes the possibility of the essential homology between the visceral loop of these forms and part of the pleuro-visceral ring of Amphineura.

The other differences between the visceral loop of most Mollusca and the pleuro-visceral ring of Amphineura are principally differences in the degree of segregation and concentration of ganglion-cells and nerve-fibres. The

pleuro-visceral ring of *Chiton* represents a very primitive nervous system, characterised by the more or less even diffusion of ganglion-cells over the whole length of the cord, while the nerves arising from it are not united into large trunks, but are given off at repeated intervals in a manner which is almost metameric. The nerves springing from it innervate the same parts of the body as the combined pleural and visceral ganglia of Gastropods and other Molluscs, *viz.*, mantle, ctenidia, intestine, heart, nephridia, and gonads. But if, after the reduction of the ctenidia to a single pair, we imagine a process of segregation to set in between these various elements, the more strictly visceral centres would become separated from the superficial pallial centres, and would assume a deeper position in the body. The law of concentration would apply in this as in other cases of evolution of nervous systems (3), and the result of the whole process would be the differentiation of a visceral nervous system, consisting of ganglia and commissural fibres, out of the primitively mixed and diffuse pleuro-visceral system. If the primitive relations to the gut and ring-like form were retained at all, they would be retained, not necessarily by the visceral system, which has *ex hypothesi* undergone considerable changes, but by the pallial (= pleural) system, which has undergone no change, except possibly one of incipient concentration.

The position of the commissural fibres of the visceral ganglion in relation to the gut becomes a matter of subordinate importance if the evolution of the nervous system has proceeded upon these lines, as will be made evident later on. As a matter of fact the visceral commissure is situated below the gut—a relation which is possibly foreshadowed in *Chiton* by a connection beneath the gut of the two gastric nerves described by Haller (8).

Pelseneer (19) indeed goes so far as to identify these gastric nerves of *Chiton* with the visceral commissure of Gastropoda and Pelecypoda; but the considerations which I

have emphasised above show that the typical visceral nerves and commissure have not yet arisen in the Amphineura; they do not arise, in fact, until the branchial, nephridial, genital and enteric branches of the primitive pallio-visceral cords are all united into one common trunk. There is some doubt, moreover, as to the existence of the gastric nerves described by Haller, since two investigators, Plate (20) and Thiele, have been unable to discover them in species of *Chiton* examined by themselves.

A valuable contribution to this part of the subject is contained in Haller's recent *Studien* (11). In the common cyclobranchiate types of Limpet the pallial nerves are separate from one another behind, and seem to be mere outgrowths of the pleural ganglia (Bouvier, 3, p. 19); but in *Lottia*, one of the more primitive monobranchiate forms, Haller shows that the pallial nerves of the two sides are directly continuous with one another posteriorly, and make a complete arch round the edge of the mantle. They are moreover not mere nerves, since they consist of a core of fibres surrounded by an outer coating—discontinuous, it is true—of ganglion-cells. They are clearly the posterior continuations of the pleural ganglia, and represent the remainder of the pallio-visceral nerve-ring of the Amphineura after the separation of the visceral elements. This view is further borne out by the existence of several connectives between the pallial ring and the pedal cords in addition to the stout ganglionic connective which in higher forms becomes the persistent pleuro-pedal connective.

The pleural ganglion.—Haller's discovery recorded in the preceding paragraph shows clearly the error of the view by which the pleural ganglion is regarded as a derivative of the pedal cords (Bouvier, Pelseneer, etc., *passim*). This view is founded on the fact that in the lower Gastropoda (Docoglossa and Rhipidoglossa) the pleural ganglia are directly continuous with the anterior ends of the pedal cords, while in the higher types the pleural ganglia

gradually move further and further away from the pedal ganglia, and, travelling along the cerebro-pleural connectives, eventually come into contiguity with the cerebral ganglia (Tenioglossa) or even fuse with them to form a single cerebro-pleural ganglion on each side (Pelecypoda).

The close connection between the pleural and pedal ganglia in the lower forms may now be interpreted in a different manner. The ganglion-cells which were primitively distributed over the whole extent of the pallial nerve-ring have been concentrated at the anterior extremities of its lateral portions, as Haller's observations on *Lottia* show—or rather in the region of the first pleuro-pedal connective, for the most anterior portion of the primitive pallial cords is represented by the cerebro-pleural connective. The shortness of the pleuro-pedal connecting piece and the great concentration of ganglion-cells which takes place at its two extremities prevent any sharp demarcation between the pleural and pedal ganglia in these lower forms; but a comparison of the nervous system of *Lottia* with that of *Chiton* (Thiele, 23, p. 387) leaves no room for doubt as to the correctness of this interpretation, which throws a flood of light upon numerous other points which have been difficult to understand upon the older views. It explains, for example, why the cerebro-pleural and cerebro-pedal connectives should be already distinct from each other in the lower Gastropods at a stage when the pleural ganglia are in actual continuity with the pedal cords, and it sets at rest the controversy as to the meaning of the lateral furrow in the pedal cords of Rhipidoglossa which has been waged with so much skill in the rival pages of the *Archives de Zoologie* and the *Bulletin Scientifique de la France et de la Belgique.*

Development of the pleural ganglion.—That the pleural ganglion is essentially distinct from the pedal is, I think, sufficiently clear from the facts of development. Although

these ganglia are placed so close together and are so intimately connected in the lower Gastropods there is not a single case on record in which the pleural ganglion has been observed to arise from the pedal ganglion, or from a common pleuro-pedal rudiment in the embryo. It is equally true on the other hand that Sarasin's derivation of the cerebral and pleural ganglia from a common rudiment in *Bithynia* (the cephalic sense-plate) has been opposed by v. Erlanger, who shows that all the great ganglionic centres arise separately, and do not become connected with one another until after their differentiation (7).

A renewed investigation of the origin of the cerebro-pleural ganglion in Pelecypoda would be of great interest in this connection. Pelseneer's (18) observations on *Nucula* have placed the fact of the composite nature of this ganglion in Pelecypoda beyond all doubt; and still, to the best of my knowledge, no one has yet observed the appearance in the embryo of a pleural element distinct from the main body of the ganglion. This apparent community of origin of the cerebral and pleural ganglia in Pelecypoda may be compared with the direct continuity of the cerebral and pleural elements of the nervous system in Amphineura.

Development of the visceral ganglia. — Sarasin endeavoured to show that the visceral ganglia of *Bithynia*, together with the pedal and abdominal ganglia, arise in the embryo from a common ventral proliferation of the ectoderm which he compares with the ventral ganglionic chain of Annelida. On this point also Sarasin has been corrected by v. Erlanger, who shows that all these ganglia arise separately from one another in *Bithynia* (7), as well as in *Paludina* (6).

The visceral ganglia are also quite distinct from the pleural ganglia in their origin, as v. Erlanger's observations show. In one important respect, however, the visceral ganglia and the pleural ganglia betray a marked similarity, the significance of which seems, however, to have escaped

the attention of its discoverer. In *Paludina* v. Erlanger figures the pleural ganglia arising from the ectoderm on each side of the body at a point just outside the velar area, but in actual contiguity with the cells of the ciliated ring. In *Bithynia* (7, Taf. xxvi., fig. 16) he figures the same condition of things for the pair of visceral ganglia. The only difference in origin between the two ganglia is that the visceral ganglia arise behind the pleural ganglia. If the Molluscan veliger possessed a nerve-ring beneath its prototroch (velum), as occurs in the trochosphere of the Annelida, it is quite clear that the pleural and visceral ganglia of *Bithynia* and *Paludina* would represent a series of ganglionic thickenings along the course of the nerve-ring. Apart from this inference, however, the topographical relations to which I have called attention seem sufficient to establish the proposition that the pleural and visceral ganglia, and, as I shall show directly, the abdominal ganglion also, of Gastropods—and, therefore, of other Mollusca—belong to a group of dorso-lateral nerve-centres quite distinct from that which is represented by the ventral or pedal cords. Here again we are reminded of the direct continuity of the pleural and visceral nerve-centres in the Amphineura.

Development of the abdominal ganglion.—In *Chiton*, as Kowalevsky has shown (15), the unpaired abdominal ganglion, or, as it is often called, the visceral ganglion, arises by a proliferation of the ectoderm at the hinder pole of the embryo, dorsally to the site of the future proctodæum. In the adult this ganglion is simply a special concentration of ganglion-cells on the supra-anal portion of the pleuro-visceral ring.

The abdominal ganglion of Gastropods is also situated at the hinder end of the visceral loop, but lies of course ventral to the gut. Can these two ganglia be regarded as homologous?

If Molluscs were mere mechanical models the answer would be undoubtedly in the negative; but embryology

points unhesitatingly to the opposite conclusion. Von Erlanger has shown that in *Bithynia* as well as in *Paludina* the abdominal ganglion develops as an ectodermal proliferation of the floor of the mantle-cavity, *i.e.*, that the ganglion is essentially a dorsal ganglion. Its final situation on the course of the sub-intestinal nerve-loop is rendered possible by the fact that its connectives with the visceral ganglia are not delaminated from the ectoderm, as are the ganglionic pleuro-visceral cords of *Chiton*, but are mere fibrous outgrowths from the ganglia themselves. Embryology is thus in complete accord with the views which have been maintained in the earlier part of this paper as to the homologies and origin of the visceral nervous system in Mollusca.

The pallial and visceral commissures in Cephalopoda.—It has long been known (Hancock) that in many Cephalopoda the stellate ganglia on the pallial nerve-cords are connected with one another above the gut by a transverse commissure. Is this commissure a relic of the pallio-visceral nerve-ring of the Amphineura and homologous with the pallial ring of *Lottia*, or is it merely a secondary connection?

In *Spirula* a remarkable arrangement of the pallial commissure has been recognised by Huxley and Pelseneer in their recent memoir (12). The commissure is not in this case a straight transverse band, but consists of two curved cords which arise from the right and left stellate ganglia respectively, and at their junction in the median line of the body give off a median pallial nerve which runs for a short distance forwards, and then passing over the anterior margin of the shell—which is, of course, internal—becomes recurrent and runs along the part of the mantle contained within the last chamber of the shell. Pelseneer is thus led to regard the commissure with its median nerve as formed by the two original pallial nerves fused together. The connection between the stellate ganglia having thus arisen in the primitive Dibranchiates (apparently in con-

nection with the reduction in size and enclosure of the chambered shell), higher forms show a series of stages in its subsequent degradation, until it is finally lost in the Octopoda. The absence of a pallial commissure in *Nautilus* also supports Pelseneer's view that in Cephalopoda this structure is not of any primary importance.

At the same time when Pelseneer added a paragraph to the effect that the supra-rectal commissure of the Amphineura is also a merely secondary junction of the pallial nerves, he was probably not yet acquainted with Haller's work on *Lottia*, and allowed his views upon the Polychæte ancestry of the Mollusca to bias his interpretation of the Molluscan nervous system.

In a recent paper on the anatomy of *Nautilus* Mr. Graham Kerr (13) also refers to the question of the supra-rectal commissure. It will be remembered that in *Nautilus* the pleuro-visceral ganglia of the two sides form a stout ganglionic band encircling the œsophagus in the region of the cerebral ganglia. The pallial nerves radiate from the lateral portions of this half-ring, and the pair of viscera nerves arise from the ventral portion. The visceral cords pass backwards on either side of the vena cava, and, after giving off the branchial nerves, are prolonged posteriorly as far as the post-anal papilla, behind which Mr. Kerr has recognised an apparent anastomosis. Mr. Kerr adds that in this case "the homologue of the pleuro-visceral cord of *Chiton* is not merely the posterior sub-œsophageal nerve-mass, but rather the two lateral portions of this, together with the post-branchial prolongations which run on either side of the vena cava. The mesial part of the posterior sub-œsophageal nerve-mass would therefore be a secondary fusion between the nerve-masses of the two opposite sides."

In his suggested homology of this possible post-anal (*i.e.*, supra-rectal) commissure of the visceral nerves in *Nautilus* with the supra-rectal "commissure" of *Chiton*,

Mr. Kerr has undoubtedly failed to appreciate the true nature of the posterior sub-œsophageal loop of *Nautilus*, as well as the relation of the visceral nerves to the pleuro-visceral cords of *Chiton*. The explanation of the Cephalopod nervous system is most readily found by comparing it with that of *Dentalium*, whose organisation in many respects supplies connecting links between that of the Cephalopoda and that of the primitive præ-torsional Gastropod or primitive Pelecypod. In *Dentalium* (22, p. 401) we find a pair of post-anal prolongations of the visceral nerves precisely resembling those described by Kerr in *Nautilus*; yet in *Dentalium*, owing to the smaller degree of concentration or cephalisation which has taken place in the nervous system, it is easy to see that the typical sub-intestinal visceral commissure exists as in Gastropods and Pelecypods. The posterior sub-œsophageal nerve-mass of Cephalopods has clearly been produced, not, as Mr. Kerr suggests, by a secondary fusion of the pleuro-visceral nerve-masses of the two opposite sides, but by a simple shortening of the visceral loop as it occurs in *Dentalium*. This would bring the visceral ganglia into continuity with the pleural ganglia and with one another,—a process of condensation with which we are already familiar in the Tenioglossa and the Euthyneura among Gastropoda.

It may here be mentioned that Willey's simultaneous account (26) of the visceral nerves of *Nautilus*, while confirming Mr. Kerr's observations as to the existence of post-anal prolongations of a pair of visceral nerves, differs from his statement as to their origin. Willey states that the nerves supplying the post-anal papilla arise independently from the sub-œsophageal visceral loop, although at their origin they are adjacent to the branchial nerves and for a large part of their course are actually contiguous with them. The significance of this separation is not remarked upon by Willey; but if the separation really exists it is certainly a difficulty in the way of his contention that the post-

anal papilla represents an approximated posterior pair of branchial sense-organs, since the anterior osphradium and both gill-plumes are all innervated from the outer visceral nerve.

Euthyneurism.—Since the publication of Spengel's paper on the olfactory organ and nervous system of Mollusca, a division of the Gastropoda into two groups, the Streptoneura and the Euthyneura, has been generally adopted. This classification has been accepted, moreover, not merely as an expression of the anatomical facts concerning the condition of the visceral loop in the two groups, but as a classification of phylogenetic significance. It is to be inferred that the two groups have been independently derived from a common type of archi-Gastropod, possessing an untwisted visceral loop—the Prosobranchs (Streptoneura) by the twisting of the loop, the Opisthobranchs and Pulmonates (Euthyneura) by the mere shortening and concentration of the untwisted loop. This view derives support from the fact that the persistent ctenidium retains its primitive position on the right side of the body in Opisthobranchs, while in Prosobranchs it shows a marked displacement and lies on the left side. Bouvier's observations on *Actæon* (= *Tornatella*), however, have completely altered the position of affairs. *Actæon* is a very primitive Opisthobranch, as may be inferred from the high development of its shell, the persistence of its operculum, and the absence of pleuropodial fins. Bouvier tell us (4) that *Actæon* resembles the Prosobranchs, not only in these points, but also in possessing a distinct twist of the visceral loop (streptoneurism, chiastoneurie). The ctenidium is innervated from a supra-intestinal ganglion, which lies on the left side of the body. We are accordingly led to the conclusion that the euthyneurous condition of Opisthobranchs and Pulmonates has not been directly inherited from the orthoneurous ancestors of the Gastropoda, but has been derived from a previously streptoneurous condition. In other words the

Opisthobranchs and Pulmonates have descended from Prosobranch ancestors, and the right-sided position of the gill-plume in Opisthobranchs is not primitive, but the result of a secondary process of detorsion.

Orthoneuroidism.—Without going further into the matter it may also here be mentioned that the supra-intestinal commissure has been recently discovered in various species of *Nerita*, *Neritina*, and *Navicella* by Boutan (2), Bouvier (3*a*), and Haller (11)—a discovery which destroys the last refuge of orthoneurism in Prosobranchiate Gastropods. Streptoneurism may now be affirmed of all Prosobranchiate Gastropods.

Origin of the Molluscan nervous system.—The attempts of previous writers to explain the relations of the nervous system of Mollusca have been based almost exclusively upon comparisons with the fully constituted nervous systems of such types as the Turbellaria and Annelida. With Thiele's theory of the Turbellarian ancestry of the Mollusca I have already dealt, and I do not propose to deal with the Annelidan hypothesis, since this theory cannot provide any satisfactory explanation of the high development of the pleuro-visceral nervous system of the Mollusca. Those authors who, like Thiele and Pelseneer, homologise both the pleural and pedal centres of the Mollusca with the ventral cords of Annelids, base their view upon the supposed origin of the pleural centres from the pedal cords. This derivation I have already shown in this article to be completely erroneous. Pelseneer's theory of the origin of the Mollusca from Polychæte ancestors (18*a*), and all theories which seek the origin of the Mollusca in the specialised representatives of any of the vermiform groups, may at once in my opinion be dismissed from consideration.

Apart from matters of minor importance it will, I think, be conceded that the following cardinal points in regard to the morphology of the Molluscan nervous system have

been established by the facts and arguments which have been presented in this article :—

(1) That the pleural ganglia have not been derived by segregation from the ventral or pedal cords.

(2) That the pleural, visceral, and abdominal ganglia of Gastropoda form a group of dorsal nerve-centres—the two former owing to their differentiation in the immediate neighbourhood of the velum, and the latter owing to its differentiation from the mid-dorsal wall of the body (floor of mantle-cavity).

(3) That the dorso-lateral nerve-ring of Amphineura is primitive and is represented in other groups of Mollusca by both the pallial and visceral nerve loops, or their derivatives.

(4) That the sub-intestinal position of the visceral loop in all groups except the Amphineura is a secondary one, which has been rendered possible only by the decentralisation of the primitive pleuro-visceral nervous system, and its separation into special ganglia and nerves, the latter being formed ontogenetically as fibrous outgrowths from the ganglionic centres.

Venturing now, in conclusion, upon more speculative ground, I believe that the embryonic relations, to which I have drawn attention, between the pleural and visceral ganglia and the ciliated band are of phylogenetic importance. It has long puzzled me that the larval forms (trochospheres) of two groups so closely allied as the Annelida and Mollusca, while presenting a close similarity in general structure, should differ so remarkably in regard to their nervous system. The Annelid trochosphere has a nerve-ring beneath its ciliated band, while the Molluscan trochosphere has none. In this respect the Molluscan trochosphere appears to be less primitive than that of the Annelida. The explanation of this now appears to me to

be as follows. In the evolution of the Annelida the prototroch and nerve-ring remained for a long time unmodified, and did not share in the elongation of the postero-ventral region of the body which gave rise to the trunk of the Annelid. This would explain the absence of the dorsal nerve-ring in the adult Annelid, provided that the nerve-ring, together with the prototroch, came to have merely a larval significance,—as actually happens in the ontogeny of Annelids to-day. On the other hand, in the evolution of the Mollusca from the same simple type of ancestor, the whole body must have shared in the elongation—the prototroch and nerve-ring as well as the more ventrally placed parts of the body. This elongated nerve-ring I identify with the pleuro-visceral ring of Amphineura, although the phyletic connection between the nerve-ring and the ciliated band is inferred from the development of certain Gastropods rather than from the Amphineura themselves. As a larval adaptation for conveniences of natation I imagine that a separation became gradually effected in embryonic life between the ciliated ring and the nerve-ring, the former becoming restricted to the anterior end of the larval body, while the latter became more and more extended *pari passu* with the elongation of the trunk. Such a separation is to some extent paralleled in the development of Holothurians from the *Auricularia* larva, as described by Semon. On this theory alone can I explain to myself the absence of the ancestral nerve-ring in the trochospheres of Mollusca, and I find some support for this view in the ontogeny of Nemertines. The lateral nerve-cords in this group have the same relation to the gut and brain as have the pleuro-visceral cords of *Chiton*, since they form a dorso-lateral ring, the posterior commissural portion passing above the rectum. In Nemertines there can be very little doubt that this nerve-ring has been derived phyletically by the elongation of a nerve-ring which underlay the ciliated band of a more or less *Pilidium*-like ancestor, as it underlies the

ciliated band of the *Pilidium*-larva, although this phyletic origin is disguised by the profound metamorphosis which breaks the continuity of the ontogenetic record in Nemertines. On this theory of course the lateral cords of Nemertines do not correspond to the ventral cords of Annelids. The latter are represented by the general ventral plexus of Nemertines and by the pedal plexus or cords of Mollusca. These ventral nervous systems appear to bear relations to the dorso-lateral ring-nerve similar to those of the subumbrellar plexus of Medusæ to the circumferential nerve-ring.

It will be recognised from these remarks that the conclusions to which I have arrived present distinct points of agreement with those of Balfour (1, p. 378) and Sedgwick (21) on the same subject, although attained throughout by an independent series of inductions. With both these writers I agree in tracing back the Molluscan nervous system to a primitively annular type, such as might be expected to exist in a Cœlenterate ancestor. Balfour derives the whole Molluscan nervous system from a peripheral nerve-ring which followed the course of a hypothetical ciliated ring; Sedgwick derives it from a broad plexus surrounding an elongated blastopore, such as occurs in existing Actinians. Sedgwick's theory was practically an alternative to Balfour's, but I find myself able to give a partial acceptance to both these views. For the nervous system of Mollusca appears to me to consist of two parts, a circumferential ring and a peri-blastoporal plexus. The circumferential ring, which was primitively associated with a ciliated ring, is represented by the pleuro-visceral nervous system, which I have shown to possess significant relations with the velum or prototroch of the larva; and the peri-blastoporal plexus seems to me to be recognisable in the pedal nervous system, which in primitive Molluscs has a very diffuse plexus-like arrangement, and in Amphineura, at any rate, reveals its peri-blastoporal character in the

cerebro-pedal connectives in front and its connectives with the supra-rectal abdominal ganglion behind.

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WALTER GARSTANG.

Report of the Hope Professor of Zoology.

By the end of the previous year it had become evident that the immense number of specimens requiring to be re-pinned and re-set would demand the attention of a special assistant for many years. Mr. Holland being occupied in arranging and classifying various parts of the Collection, in separating various sections for the work of others, and in looking out specimens to illustrate lectures, could devote but little time to this necessary labour. I therefore decided to employ a junior assistant for this purpose, and after much consideration, engaged H. Smith of Reading, who had already acquired considerable experience in manipulating the British Lepidoptera and Coleoptera. He began work towards the end of January, and by the end of the year had made considerable progress, especially with the Lepidoptera Heterocera.

The British Lepidoptera which had been commenced by Mr. Holland in the previous year, were completed, except the staging of the minute species. In the general collection the *Sphingidae*, *Noctuinae*, *Geometrinae*, *Bombycinae*, *Syntomidae*, *Psychidae*, *Arctiidae*, *Agaristidae*, *Zygaenidae*, *Castniidae*, and *Uranidae* were completed, with the exception of those American specimens which had been adjusted by Mr. Holland in 1894. Among the Lepidoptera Rhopalocera the majority of the *Euploeinae*, *Danainae*, *Acraeinae*, and *Heliconinae* were also re-set. A considerable amount of printing was also undertaken by H. Smith during the latter part of the year.

Mr. Holland named and classified the general collection of *Sphingidae*, arranging nearly the whole of it in three small cabinets containing altogether fifty drawers. When this arrangement has been completed by the addition of printed

locality and type labels, together with coloured geographical labels, the *Sphingidae* will constitute an exceedingly fine and valuable collection, in every way available for convenient reference.

Mr. Holland has also named and classified the *Zygaenidae* and *Syntomidae*, so that these groups are ready to be arranged. He also in large part worked out the *Heliconinae* and *Heliconoid Danainae*. Many of the more obscure species were taken to London and compared with the splendid Godman-Salvin Collection. I wish to express my sincere thanks to these gentlemen and to the heads of the Insect Department of the British Museum for their invariable courtesy, and for their kindness not only in granting me free access to the Collections, but in bestowing much time and trouble in helping to compare and identify the species. I am glad to think that we have been enabled in some slight degree to return this kindness by bringing a few of the types, and other specimens of the greatest interest, to London for examination and study. I wish also to thank Mr. W. F. H. Blandford and Mr. Champion for their kind help in the comparisons with the Godman-Salvin Collection.

Mr. Schaus completed his work upon the American moths, and his valuable catalogue of the types in the Hope Collection will be published during the present year.

Dr. Dixey has been arranging the *Pierinae* in the finest of the cabinets purchased for the Department in 1894, adding the geographical labels and maps, and making out the most obscure groups.

Mr. Sidgwick has continued his arrangement of the British Lepidoptera, and towards the end of the year has been helped by Mr. Pogson Smith. The butterflies and the larger moths are already arranged, and this part of the Collection has been found very useful by undergraduates and others who have consulted it in order to name their specimens.

Col. Swinhoe has continued his work upon the Oriental Heterocera, and the arrangement of this part of the Collection.

In the rearrangement of the cabinets in the enlarged Hope Museum, three very conspicuous and unsuitable cabinets were

removed, the sale of the old cases assisting to provide new ones for the old drawers. The new cases were made of such dimensions as to bring several cabinets in the Museum up to a uniform height.

On the upper floor the east room has been fitted up as a biological laboratory, and Mr. and Mrs. Garstang have worked in it since October.

In Lent Term the course of Lectures on 'Charles Darwin and the Problems of Modern Biology' was continued ; and in Michaelmas Term a course upon 'Mimicry' was begun.

Additions to the Collection :—

Owing to the confusion caused by the building operations, several additions to the Collection made in 1894 escaped record in the Report of that year. They are accordingly inserted in this year's Report.

Donations in 1894 (not included in Report of that year):—

Lepidoptera Rhopalocera (23 specimens), from various localities, presented by G. C. Griffiths, Esq.

An example of a species of Acridiidae from Egypt, presented by A. J. Butler, Esq., M.A.

A series of Leucophasia sinapis (8 specimens), from Reading, presented by Mr. W. Holland.

A valuable series of Orthoptera (21 specimens), from various localities, presented by M. Henri de Saussure.

Purchases in 1894 (not included in Report of that year) :—

A valuable series of Danainae and Acraeinae (226 specimens), from various localities, from the Collection of the late J. Jenner Weir, Esq., purchased at Stevens'.

Donations in 1895 :—

Lepidoptera Rhopalocera (17 specimens), captured in 1894 by F. E. Pollard, Esq., at Etshowe, Zululand, presented by Miss Pollard.

Rare Coleoptera (6 specimens), from Sussex, presented by J. H. A. Jenner, Esq.

Lepidoptera (115 specimens), chiefly Rhopalocera, from the Khasia Hills, India, presented by Col. Swinhoe.

Parnassius mnemosyne (2 specimens), from the Pyrenees, presented by H. M. Wallis, Esq.

Myriapoda, Arachnida, and Insecta (58 specimens), chiefly Lepidoptera, from Teneriffe, presented by Mrs. Holt White.

Purchases in 1895:—

Lepidoptera (almost exclusively Rhopalocera), and one specimen of a Coleopterous species (647 specimens), chiefly from Venezuela and Colombia, purchased from Watkins and Doncaster. The great majority of the specimens will form the nucleus of a special Collection illustrating Mimicry.

Lepidoptera Rhopalocera (6 specimens), from Africa, purchased from E. Swinhoe.

Professor Westwood's private Collection, containing about 1450 Lepidoptera and about 300 Coleoptera (captured by General Hearsey in India), purchased from Miss Swann.

THE HOPE LIBRARY.

Many necessary works of reference were purchased during the year, including the parts of Barrett's 'British Lepidoptera' and Saunders' 'British Hymenoptera aculeata.'

The following works were presented by Professor Poulton:—

Eight volumes of the Ray Society, 1885 to 1892 inclusive.

Transactions, Entomological Society, from 1893 to 1895 inclusive.

Transactions and Journal of Linnaean Society, from 1893 to 1895 inclusive.

Vols. i to vi (inclusive), vol. viii, vols. xv to xxix (inclusive) of the Zoological Record, thus completing the series in the Library.

The first four volumes of The Entomologist's Record, from its beginning in 1890.

Weismann's Essays on Heredity, two vols., Oxford, 1891, 1892.

Butterflies and Moths of Teneriffe, by A. E. Holt White, one vol.

Catâlogue of the Library of the Entomological Society of London, one vol.

Tertiary Rhynchophorous Coleoptera (one vol.), presented by the author, S. H. Scudder, Esq.

The Spiders of Burmah (one vol.), presented by the Trustees of the British Museum.

Indian Forest Zoology (one vol.), and the volume on Silk, No. 23 of the Handbooks of Commercial Products, presented by the author, E. C. Cotes, Esq.

Revisio Insectorum Familiae Mantidarum, by the late Prof. Westwood (one vol.), presented by Miss Swann.

The Parts of the work on Membracidae in the Biologia Centrali-Americana, published during the year, presented by the author, Canon W. W. Fowler.

A copy of Diversae Insectarum Volatilium, by D. I. Hoefnagel (1630), presented by T. W. Taphouse, Esq.

Copies of Original Papers were also presented to the Library by the following authors:—Baron Osten Sacken, E. E. Austen, Esq., G. H. Carpenter, Esq., F. Heron, Esq., Rev. T. R. R. Stebbing, F. A. Bellamy, Esq., Prof. Sigismondo Orlandi, J. W. Shipp, Esq., C. O. Waterhouse, Esq., M. Henri de Saussure, Prof. Enzio Reuter, Rev. E. N. Bloomfield, A. G. Butler, Esq., G. F. Hampson, Esq., and S. H. Scudder, Esq.

A very complete and numerous set was presented by W. F. Kirby, Esq.

The University of Genoa presented copies of the Reports of the Museum of Comparative Anatomy.

The Bombay Natural History Society and the Boston Society of Natural History presented their publications for the year.

EDWARD B. POULTON.

Report of the Hope Professor of Zoology.

THE year 1896 was an extremely successful one for the Hope Department; for large and valuable presents have been received, and a great deal of work has been accomplished, not only by the staff, but also by many friends who have kindly helped in their special lines of research.

Thus the whole Collection of British Aculeate Hymenoptera has been revised by Mr. Edward Saunders; a part of the Collection of Phytophaga (Coleoptera) by Mr. M. Jacoby; the Membracidae and Cicadae by Canon Fowler, assisted by Mr. W. F. Kirby. In order to render this kind and valuable help possible the specimens were sent to the gentlemen named above, but nearly all of them have now been returned.

Much help has also been received from friends who have visited the Department. Mr. Philip P. Calvert of Philadelphia assisted in making out Rambur's types of Odonata; Mr. Roland Trimen, F.R.S., and Mr. G. A. K. Marshall with the African Rhopalocera; Col. Bingham with the general Collection of Aculeate Hymenoptera; Mr. G. A. Boulenger, F.R.S., with the Collections of fishes, amphibia, and reptiles.

Among residents Dr. Dixey has continued his arrangement and study of the Pierinae, Col. Swinhoe of the Oriental Heterocera, Mr. Arthur Sidgwick and Mr. Pogson Smith of the British Lepidoptera.

Mr. Sidgwick kindly presented the Department with a fine set of entomological forceps.

Mr. A. W. Pickard-Cambridge began the revision of the British Coleoptera, but was prevented from carrying on the work by the pressure of other duties.

It is my pleasant duty to thank all the eminent entomologists I have named for their kind help to the Department and the University.

Mr. and Mrs. Garstang have continued to work, principally upon Crustacea, in the East Laboratory, for which a Jung

microtome was purchased, the expense being defrayed by the Common University Fund.

The event of the year has been the generous gift of a large Collection of butterflies by Mr. Godman and Mr. Salvin. A general description of the Collection and the work which has been done upon it, will be found in the account of the additions to the Department during 1896. The selection and packing of the specimens for conveyance to Oxford required many visits to London by the Professor, Dr. Dixey, and Mr. Holland.

The work on the Collections also necessitated many journeys to London, for comparison with the specimens in the British Museum and the Godman-Salvin Collection. I wish to thank the Head and Assistants in the Insect Department of the former, and Mr. Godman, Mr. Salvin, and Mr. Champion, for their invariable kindness.

The Council of the Entomological Society of London were invited to visit Oxford, June 27–29, and I am pleased to say that many of them were able to be present, including the President, Professor Meldola, F.R.S., the Treasurer, Mr. R. McLachlan, F.R.S., Mr. Salvin, F.R.S., Mr. Trimen, F.R.S., Mr. Blandford, and Mr. Champion, as well as the members resident in Oxford. Many kind friends helped to offer hospitality to our visitors. The Hope Collections were inspected, and will benefit very greatly from the valuable suggestions made by the eminent authorities who were present. While the visit was in every way a great pleasure and advantage to us in Oxford, it is very satisfactory to learn from the allusion in the Presidential Address to the Society (Jan. 1897) that it was also enjoyed by our visitors.

Now that the visit of the Council, to which I have long looked forward, has taken place, I trust that it may be repeated annually.

During the year Mr. Holland has been engaged in naming and arranging many sections of the butterflies, in making out the forms of labels for printing in the Department, and in looking out, arranging and numbering the specimens to be sent to those who have helped us. During the latter half of the year, the Godman-Salvin specimens have been brought to Oxford, and much of Mr. Holland's time has

been occupied in working them out and arranging them, parallel with the corresponding groups in the Hope Collection. The work already done is indicated in the table printed in the description of this gift. Earlier in the year the general Collection of Danainae was in large part arranged in a final form, with coloured labels indicating the geographical distribution, &c.; but the great additions which were made later in the year, made it necessary to postpone this work for a time.

A large amount of re-pinning and re-setting was done by H. R. Smith, so that all the groups of butterflies, with the exception of the Papilioninae, the Hesperidae, and part of the Nymphalinae Lycaenidae and Erycinidae, are now finished. The very numerous specimens added to the Department during the year have also been set, with the exception of parts of the Godman-Salvin gift indicated in the table printed in the account of this Collection.

At the beginning of 1896 it was decided after much consideration to modify the style of setting in order to bring it into harmony with that now adopted in the British Museum, and other great Collections in this country. The specimens are now set with the wings as flat as possible, and are raised high on the pin; so that there is abundant room for small labels below the insect itself. In order to carry out this change, a set of new boards was purchased, and a considerable amount of Smith's time was devoted to making others.

Furthermore, many hundreds of label-holders were screwed on to the fronts of cabinet drawers, a certain number of drawers were re-papered, and several shelves were fixed in the small East Laboratory. Hence, with a large amount of label-printing, especially in connexion with the specimens added during the year, Smith's time was very fully occupied.

In Lent Term the Professor lectured upon "Mimicry"; in the Summer Term he gave two Public Lectures on "The Hope Collections." There were no lectures during Michaelmas Term.

Additions to the Collection :—

A very valuable Collection of Rhopalocera (butterflies), chiefly from Central and South America, but also including a large number from other parts of the world, was presented

by F. Ducane Godman, Esq., F.R.S., and Osbert Salvin Esq., F.R.S. This important Collection, constituting by far the largest accession to the Department during recent years, was formally accepted by a Decree of Convocation on May 11, 1897, when the further Decree conveying the thanks of the University to the Donors was also passed unanimously.

The specimens were however presented and brought to Oxford during 1896, and the work upon them occupied a large part of the Assistants' time, so that they are best included in the Report of that year. The following account, reprinted from the *University Gazette* for April 30, 1897, affords a brief description of this valuable gift, and also indicates the nature of a large part of the work upon which the Hope Department was engaged during the second half of 1896, and the special needs of the Department at the present time.

"*Note.*—The following note has been prepared by the Hope Professor, explaining the value of the Collection and the expenditure which may be caused by its acceptance:—

The specimens in this Collection are of especial value because of the excellent geographical data which accompany them. Although specimens from all countries are included, the Collection is especially rich in species from Central America, a district of peculiar interest, hitherto but poorly represented in the Hope Collection. Many specimens of historic interest are also present—the captures of H. W. Bates in Brazil, of T. Belt in Nicaragua, and of A. R. Wallace in the Malay Archipelago. The majority of the more recently captured specimens were taken by the greatest living collectors, such as G. C. Champion and H. H. Smith (Central America), and C. M. Woodford (Solomon Islands); so that all localities can be entirely depended upon. No conditions are attached to the gift, so that the specimens can be at once incorporated with those of the General Collection, as soon as they have been adequately labelled.

The Collection also contains a large amount of material which will be available to illustrate the principles of Protective Mimicry, Geographical Distribution, Isolation, &c.

The following table indicates the numbers of specimens now in Oxford. The numbers of all Groups which are

marked as 'named' are final: those of the others will be somewhat reduced when they have been named and compared with the existing Collection:—

Families of Rhopalocera.	Number of Specimens.	Work accomplished.
1. NYMPHALIDAE—		
a. *Danainae* ...	2,142	Named, arranged, re-set.
β. *Satyrinae* ...	1,677	Named, arranged, re-set.
γ. *Elymniinae* ...	18	Named.
δ. *Morphinae* ...	153	Named.
ε. *Brassolinae* ...	163	Named.
ζ. *Acraeinae* ...	256	Named, arranged, re-set.
η. *Heliconinae* ...	513	Named, arranged, re-set.
θ. *Nymphalinae*...	5,311	Named, partially arranged and re-set.
2. ERYCINIDAE... ...	1,182	Named, arranged, re-set.
3. LYCAENIDAE... ...	995	
4. PAPILIONIDAE—		
a. *Pierinae*... ...	2,151	Mostly re-set.
β. *Papilioninae*...	1,092	Named.
5. HESPERIDAE... ...	463	
TOTAL	16,116	

As regards the Old-World species in the above-named Groups, the whole of the duplicates of the Godman-Salvin Collection have been placed at our disposal; but as regards the New-World species, Mr. Godman and Mr. Salvin kindly promise that further specimens will be available in the future.

The approximate value of the gift is very difficult to estimate. In the autumn of 1895 the Department purchased 522 specimens of South American Lepidoptera for £21—a sum which was evidently considered to be exceptionally small and was only arrived at after much discussion. Many of the specimens in the Hope Department, selected by the late Professor, still retain the price upon their labels, proving that 2*s.* 6*d.* or 3*s.* 6*d.* apiece was paid for them. The Hope Collection contains some few (perhaps a dozen) specimens from the Solomon Islands, purchased by Professor Westwood at a cost of from 3*s.* 6*d.* to 10*s.* 6*d.* apiece: whereas among the Godman-Salvin specimens there are 826 specimens from this locality, captured by C. M. Woodford, but of far greater scientific value, in that several islands of the Group are represented, including the extremely dangerous Maleita

Island, where the collector could not venture beyond the range of the rifles of his guard. The few Hope specimens, also captured by C. M. Woodford, are all from the best-known island, Guadalcanar. The South and Central American specimens, constituting by far the greatest part of the Collection which is now presented, are of much greater scientific value than those which were purchased in 1895, and than the majority of the Hope specimens from the same localities, because of the greater accuracy and precision of their geographical data. To obtain specimens with such data it would be necessary again to send out, and maintain on the spot for many years, the best living collectors. From these considerations some conception of the great value of the gift may be arrived at.

The cost involved in the acceptance of the gift is as follows:—

(1) *Transfer of specimens to Oxford.*

This has been paid for out of the income of the Hope Department, and amounts to about £15. [The cost was under £12. E. B. P., May 14, 1897.]

(2) *Re-setting, printing, naming, arranging.*

Most of this work has been done: it will be completed (including the printing) by the Departmental staff without any extra expense to the University.

(3) *Cabinets.*

New cabinets are imperatively needed for the present Collections, which are densely overcrowded; and apart from the Godman-Salvin gift, it would have been necessary for me to apply soon to the University for a grant nearly as large as may be involved by its acceptance, for a large proportion of these specimens will occupy the spaces which would have been necessarily left blank in the rearrangement of the present Collections, while others will replace specimens which are in bad condition.

The right arrangement now would be to raise a sum of £600 for the purchase of 10 cabinets of 60 drawers, each made in 3 sections of 20 drawers, all the drawers to be made interchangeable. I have already concluded a contract with

a well-known London maker to supply half this number, with the option of taking the second half at the same rate. Towards this sum the Delegates of the Museum have voted £100, and the Delegates of the Common University Fund £100. I have raised by subscriptions about £200, and it is possible that I may obtain £250 in this manner. There remains £150, which I trust may be raised in some way. If however this sum cannot be obtained, I shall make the best possible use of the funds which are now available, although this will involve ultimate expense in consequence of the adoption of a more crowded arrangement. The careful work which is necessary for insect-cabinet-making is necessarily very slow, and consequently the £150 will not be required until the autumn, or perhaps the beginning of next year."

The following copy of one of the labels printed in the Hope Department, serves to indicate the information which will be available upon each of the specimens as it is incorporated in the general Collection.

AOLA
Guadalcanar
Solomon Islands
Capt. March 30.
to Sept. 25. 1887.
byC.M.Woodford.
Ex Godman-Salvin
Coll., Pres. 1896
by F.D.G.and O.S.

The contributions which have been promised or paid to the fund for the purchase of new cabinets are as printed below. I am glad to take this opportunity of thanking those who have helped to overcome the great difficulties of the present position. Further assistance is much needed.

	£	s.	d.
George Palmer, Esq.	50	0	0
G. W. Palmer, Esq.	20	0	0
A. Palmer, Esq.	20	0	0
The Principal of Brasenose College	10	0	0
Prof. Poulton	50	0	0
E. Chapman, Esq.	5	0	0
Dr. G. B. Longstaff	25	0	0
Capt. J. W. Woodall	5	0	0

The Department has also received many other valuable accessions during 1896. The large numbers of Rhopalocera, kindly presented by A. G. Cardew, Esq., J. J. Walker, Esq.,

R.N., and G. A. K. Marshall, Esq., are of especial value because of the accurate data which accompany them. Those of Mr. Marshall are accompanied by notes giving precise date, locality, height above the sea, and statement as to wet or dry season form. They are the most perfectly recorded specimens in our whole Collection.

The specimens presented by A. G. Cardew, Esq., consist of 398 specimens of Rhopalocera from the Nilgiri Hills and Cannanore; and 36 Heterocera from Nilgiris, 4 from Cannanore, 1 from Madras, and 1 from Coimbatore. I have already alluded to the excellent data which accompany the specimens.

J. J. Walker, Esq., R.N., presented a very valuable set of 579 specimens of Rhopalocera, 20 Heterocera, 59 Coleoptera, and 4 Oceanic Hemiptera (Hylobates). Nearly all the specimens were captured by Mr. Walker in the countries visited during the Voyage of H.M.S. "Penguin" (1890–93), and during other voyages. The specimens are chiefly Oriental and Australian, although there are some valuable additions from Central and S. America, S. Europe, and the Levant. The data accompanying the specimens are most excellent. The Rhopalocera include the very rare *Eroessa chilensis* (new to the Department), and a fine series of Polynesian forms of *Hypolimnas bolina.*

The 714 specimens of Rhopalocera presented by G. A. K. Marshall, Esq., were all captured by him in S. Africa. The admirable condition of this valuable series has been already described.

Forty-two specimens of Danainae and 54 of Euploeinae were presented by Col. Swinhoe.

Two specimens of *Limnas Klugii* were presented by C. A. V. Peel, Esq., captured by him in Somaliland.

Fifty-three specimens of Lepidoptera, chiefly Oriental, were presented by Professor Poulton. These specimens are chiefly intended to illustrate "Mimicry."

Twenty-eight specimens of Rhopalocera were presented by O. V. Aplin, Esq., captured by him in Soriano (Uruguay), the Sahara, and Arctic Norway.

A valuable set of 297 specimens from various localities, chiefly of Rhopalocera, but also containing examples of

Heterocera, Diptera, Neuroptera, and Orthoptera, were presented by G. C. Griffiths, Esq.

A curious form of *Heliconius erato* from British Guiana was presented by Mr. A. H. Hamm.

The Collections of British Insecta were also enriched during the year. As regards the Lepidoptera, a series of 12 *Hesperia lineola* from Sheerness were presented by J. J. Walker, Esq., R.N.; 2 specimens of the very rare *Platypteryx Sicula* (from the Leigh Woods, Clifton), 1 specimen of *Sesia scoliaeformis* from Rannoch, and a series of 20 *Acidalia holosericata* from Clifton, were presented by G. C. Griffiths, Esq.; a series of 7 *Catocala promissa* from Lyndhurst by C. A. V. Peel, Esq. Professor Poulton also presented 3 British specimens of *Vanessa antiopa* ("Camberwell Beauty"), 2 captured at Cromer in 1872, and 1, a hybernated specimen, captured near Reading in the spring of 1873; his son, Edward P. Poulton, presented an extremely small specimen of *Lycaena argiolus*, and 2 rare or local moths,—captured by him at St. Helens, Isle of Wight.

Among the other Orders of British insects, the Orthoptera were enriched by a series of 10 *Periplaneta americana* from the Zoological Gardens, and a specimen of *P. australasiae* from Kew, presented by Malcolm Burr, Esq.; while the Neuroptera received an addition of 9 specimens of Odonata from the neighbourhood of Oxford, presented by H. R. Smith.

There were comparatively few purchases of specimens during the year. Four specimens of *Papilio meriones* from Madagascar, and 3 Oriental species of *Eusemia*, being the only additions obtained in this way during 1896.

A few additions to the Collection of British Birds made in 1895, omitted from the Report of that year, are now included.

Bittern (Botaurus stellaris) ♂, shot and presented by Mr. T. Dewe, of Longworth, January 10, 1895, at 7 p.m., while duck shooting on land in the occupation of Mr. Chandler, at Duxford, 6½ miles N.E. of Faringdon, Berks.

Young Land-rail (Gallinula crex) ♂. Age 6 to 8 weeks. Taken at Shippon, near Abingdon. Presented by Mr. H. Trim, University Museum. July 15, 1895.

Little Auk (Mergulus melanoleucos) ♀, shot on Port Meadow, Oxford, while diving in the floods, in January, 1895, by E. Mott, from whom it was purchased.

THE HOPE LIBRARY.

Miss Swann presented 4 lithograph portraits of naturalists, a set of coloured sketches of flowers, and a large number of valuable manuscript notes by the late Professor Westwood, and 2 volumes and 1 pamphlet which belonged to him.

Two valuable books containing manuscript notes by Sir Sydney Saunders, on his collection of Hymenoptera, now in the Hope Department, were presented by Edward Saunders, Esq.

The Transactions of the Entomological Society, and the Transactions and Journal of the Linnaean Society for the year 1896, were presented by Professor Poulton.

The Biological Department of the Owens College, the Bombay Natural History Society, the Boston Society of Natural History, the Chicago Academy of Sciences, the Zoological Museum of the University of Genoa, presented their publications for the year. The Radcliffe Library presented the Catalogue of Books added during 1896. The New York State Museum presented its Report for 1894. The acknowledgement was inadvertently omitted in the Report for the year.

Canon W. W. Fowler presented the Parts of his monograph on the Membracidae in the Biologia Centrali-Americana, published during the year.

Several volumes and pamphlets formerly in the Ashmolean Museum were transferred to the Department, including a very fine Buffon's Natural History in 127 volumes.

A few volumes and pamphlets from the Proceedings of the Ashmolean Society were given to the Department.

Copies of Original Papers were also presented to the Library by the following authors:—Rev. T. R. R. Stebbing, Sir George F. Hampson, Bart., S. H. Scudder, Esq., Col. Swinhoe, Hamilton Druce, Esq., Edward Saunders, Esq.,

C. O. Waterhouse, Esq., Dr. Fritz Müller, Rev. E. N. Bloomfield, A. G. Butler, Esq., Mons. P. Lesne, Dr. and Mrs. G. W. Peckham, Baron Osten Sacken, G. A. K. Marshall, Esq., Lord Walsingham, Peter Cameron, Esq., Prof. R. Warington, and P. P. Calvert, Esq.

A few volumes and pamphlets were purchased for the Library, including a fine coloured copy of the "Thesaurus" of Professor Westwood. The serial works purchased in previous years were continued.

EDWARD B. POULTON.

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